Morphology and Evolution of Sesamoid Elements in Bats (Mammalia: Chiroptera)

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ABSTRACT

Sesamoids are skeletal elements found within a tendon or ligament as it passes around a joint or bony prominence. Here we review the distribution of sesamoids in bats, the only mammals capable of powered flight. Our survey included bat species representing most extant families as well as two key Eocene fossil bats in which sesamoids are exquisitely preserved, *Onychonycteris finneyi* and *Icaronycteris index*. We identified 46 separate sesamoid elements (or sets of elements) from dissections of selected bat taxa, with no more than 23 of these present in any given species. Among the sesamoids identified in our survey, 12 have not previously been described in bats. We also identified seven sesamoids previously described in the literature that are not present in our sample of species. No sesamoids were found to be exclusive to the fossil taxa in our study; all the sesamoids observed in *Onychonycteris* and *Icaronycteris* have apparent homologs among extant species. We mapped the presence/absence of the 46 sesamoids onto a bat phylogeny. Based on these optimizations, we discuss homology issues and evolutionary history of some of the most taxonomically widespread sesamoids. Functional inferences regarding some sesamoids can be made based on what is known about bat musculoskeletal morphology, although further biomechanical studies are required to test the hypotheses proposed here. Sesamoids will continue to be a source of interesting insights about the evolution of bats and their unique locomotor abilities.

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INTRODUCTION

Sesamoids are typically defined as bones found within a tendon or ligament as it passes around a joint or bony prominence (Retterer and Lelièvre, 1911; Pearson and Davin, 1921a, 1921b; Romer, 1956; Haines, 1969; Le Minor, 1987; Sarin et al., 1999; Maisano, 2002; Jerez et al., 2010; Vera et al., 2015; Regnault et al., 2016). However, ossification is not essential; more broadly speaking, sesamoids are "any organized, intratendinous/intraligamentous structures, including those composed of fibrocartilage" (Regnault et al., 2017: 2; see also Haines, 1969; Tsai and Holliday, 2011). Sesamoids occur in tendons associated with a large number of mobile joints in vertebrates, most commonly in the postcranium (e.g., Romankowowa, 1961; Ponssa et al., 2010; Jerez et al., 2010; Chadwick et al., 2014; Regnault et al., 2014; Reyes-Amaya et al., 2017; Samuels et al., 2017) but also in the cranium of some taxa including many bony fishes (e.g., Alexander, 1967; Adriaens and Verraes, 1998), crocodiles and turtles (Tsai and Holliday, 2011), birds (Hall, 2005), and lizards (Montero et al., 2017). Although the study of sesamoids has been neglected historically, these structures are a source of several acute clinical problems in animals, including humans, significantly impairing proper musculoskeletal function when abnormally developed or diseased (Skillern, 1915; Bizarro, 1921; Gunn, 1928; Streatfeild and Griffiths, 1934; Sindberg, 1940; Stener, 1963; Helal, 1981; Wood, 1984; Goldberg and Nathan, 1987; Hansen and Peterson, 1987; McBryde and Anderson, 1988; Gibeault et al., 1989; Bianchi et al., 1993; Richardson, 1999; Mellado et al., 2003; Mittlmeier and Haar, 2004; DeCamp, 2016).

The best-known sesamoid is the patella (= kneecap), which is located in the primary extensor tendon associated with the knee joint in many but not all tetrapods (Reese et al., 2001; Samuels et al., 2017). The patella is absent as a bony structure in several groups of reptiles and amphibians, most marsupial mammals, and in a few species of birds and eutherian mammals, but it is present as a fibrocartilage structure in many of these taxa (e.g., Smith et al., 1995; Chadwick et al., 2014; Samuels et al., 2017; Abdala et al., 2017). In contrast, the ulnar patella, a sesamoid associated with one of the primary joints (sensu Pomikal and Streicher, 2010) of the forelimb—the elbow—is apparently normally present among mammals only in bats (Gunn, 1928; Haines, 1940; Mittal et al., 2014). Jerez et al. (2010) proposed a classification of sesamoids based on their relationships to the tendons and joints with which they are associated. The patellae (both the kneecap and the ulnar patella of bats) constitute examples of "embedded sesamoids" that are intimately associated with tendons, being entirely surrounded by tendinous tissue. Some of the most powerful muscles of the limbs (e.g., the quadriceps) with tendons wrapping around bony prominences or joints are associated with embedded sesamoids (Jerez et al., 2010). Other categories identified by Jerez et al. (2010) include "supporter sesamoids" that serve as muscle-attachment areas (e.g., the pisiform), and "glide sesamoids" that provide smooth gliding surfaces for the flexor tendons in manus and pes.

The functions of sesamoids have been a matter of speculation for decades. Sesamoids have generally been thought to function in association with the mechanical stress exerted on tendons as they wrap around a bony edge or a joint, possibly improving the ability of these tendons to respond to compressive load, pressure, tensile strain, and vibration (Carlsöö, 1982; Pearson and Davin, 1921a, 1921b; Nussbaum, 1982; Sarin et al., 1999; Jerez et al. 2010; Ponssa et al., 2010; Tsai and Holliday, 2011; Otero and Hoyos, 2013; Regnault et al., 2016; Abdala et al., 2017; Zhang et al., 2017).

Enhanced or improved function may also be achieved by altering the moment arm of the related tendon, thus increasing the mechanical advantage of the muscle-tendon unit (Alexander and Dimery, 1985; Vickaryous and Olson, 2007; Regnault et al., 2014). Evans and De Lahunta (2013) summarized three primary potential functions of sesamoids: (1) to protect tendons that pass over bony prominences; (2) to increase the surface area for attachment of tendons over certain joints; and (3) to redirect the pull of tendons so that greater effective force can be applied to the part being moved. It is possible and indeed likely that at least some sesamoids have multiple functions, acting in different ways during different phases of locomotion, e.g., the human patella may play a different role during standing than it does during active limb extension (Mottershead, 1988).

A controversial subject has been the development of sesamoids, and how this relates to their evolutionary origins. Many authors have assumed that sesamoids form de novo within tendons in response to stresses associated with joints (e.g., Müller and Wagner, 1991; Newman and Müller, 2000; Müller, 2003). Alternatively, other authors have emphasized a potential link between epiphyses and sesamoids. Parsons (1904) first proposed the concept of "traction epiphyses," an idea subsequently supported by Barnet and Lewis (1958) and other authors (e.g., Hogg, 1980; Hutchinson, 2002; Hall, 2005; Vickaryous and Olson, 2007; Ponssa et al., 2010; Regnault et al., 2014) as an explanation for the origin of some epiphyses in tetrapods. The traction-epiphysis hypothesis suggests that preexisting intratendinous sesamoids could fuse to the end of a long bone and become part of the epiphysis. Conversely, Pearson and Davin (1921a, 1921b) proposed a reverse process in which sesamoids originate from bone processes that become separated from the main bone. Recent studies using new histological and molecular data in mammalian taxa (e.g., Koyama et al., 2010; Eyal et al., 2015) have suggested that different developmental pathways may apply to sesamoids (or sets of sesamoids) associated with different joints, and that multiple pathways related to sesamoid development hence might cooccur in the same organism.

Bats (order Chiroptera) are the only mammals capable of powered flight (Norberg and Rayner, 1987). In all mammals that use aerial locomotion (i.e., gliders and powered flyers), the airfoil consists of skin membranes known as patagia that minimally extend between the fore- and hind limbs (Norberg, 1972). In bats, airfoil area is increased by the presence of the dactylopatagium (= handwing) consisting of interdigital membranes supported by elongated fingers (e.g., Sears et al., 2006; Hockman, et al., 2008). This highly derived forelimb structure is accompanied by the modification of many muscles of the forearm and hand into largely tendinous structures that are often associated with sesamoids, especially near their points of insertion (Vaughan, 1959; Romankowowa, 1961; Norberg, 1972; this study). Sesamoids are numerous in bats and their association with the flight apparatus has intrigued researchers for over 100 years; as a result, bats have been highlighted in many studies of sesamoids (e.g., Parsons, 1904; Haines, 1940; Oxnard, 1971; Alexander and Dimery, 1985; Le Minor, 1994; Bland and Ashhurst, 1997). Bat sesamoids have also been described in the context of anatomical studies of both extant and fossil bat taxa (Macalister, 1872; Vaughan, 1959; Romankowowa, 1961; Cypher, 1996; Walton and Walton, 1970a, 1970b; Norberg, 1972; Simmons and Geisler, 1998; Simmons et al., 2008; Panyutina et al., 2015; Reyes-Amaya et al. 2017). However, studies dealing exclusively with bat sesamoids are scarce and largely have centered on the distal wing (Romankowowa, 1961; Cypher, 1996). An orderwide review of sesamoid structures across the entire

bat skeleton is lacking. To address this gap in our understanding, in this study we present a systematic review of bat sesamoids including new data on several sesamoids not previously described in Chiroptera. Our goals were to provide a review of the previous literature on bat sesamoids, to survey the postcranial sesamoids across bat families, and to assess the evolutionary history of selected sesamoids or sesamoid traits that vary interspecifically and may have important functions relevant to various flight modes. We included in our analysis data on sesamoids from two exquisitely preserved bat fossils, *Icaronycteris index* (Jepsen, 1966) and *Onychonycteris finneyi* (Simmons et al., 2008), which together with our data on representative extant taxa, allow us to infer patterns of acquisition and loss of sesamoids in Chiroptera.

MATERIALS AND METHODS

In order to compile a list of the postcranial sesamoids thus far described for bats, we reviewed the literature on bat myology and osteology (i.e., Macalister, 1872; Vaughan, 1959; Romankowowa, 1961; Walton and Walton, 1970a, 1970b; Vaughan and Bateman, 1970; Norberg, 1972; Cypher, 1996; Panyutina et al., 2015; Reyes-Amaya et al., 2017). Homologies of sesamoids described in different sources were hypothesized primarily using the criterion of topological similarity, i.e., two sesamoids were considered homologs if they were located in the same tendon of the same muscle or in the same ligament. This positional criterion is the conventional means used to infer sesamoid homologies (e.g., Pearson and Davin, 1921a, 1921b; Le Minor, 1987; Vanden Berge and Storer, 1995; Olson, 2000; Hall, 2005; Kawashima et al., 2007; Vickaryous and Olson, 2007; Kim et al., 2009; Jerez et al., 2010; Ponssa et al., 2010; Abdala et al., 2017; and Samuels et al., 2017).

Muscle nomenclature used in this study follows Vaughan (1959). To describe sesamoid locations, the following synonymies of directional terms were applied: (1) medial = preaxial = radial/tibial; (2) lateral = postaxial = ulnar/fibular. These terms were applied to both the forelimb and hind limb to avoid misunderstandings when comparing bat sesamoids to those of other tetrapods. In bats, the hind limbs are rotated 180° relative to their position in other mammals (Simmons, 1994), so proper terminology is crucial. In the hand (= wing) and foot, the dorsal (extensor) and the palmar (flexor) surfaces are equivalent with those of the limbs of other mammals, so the terms applied are the same. Finally, we applied the term "lunulae" to those sesamoids that, based on their locations, are presumably derived from an ossified meniscus (e.g., Jerez et al., 2010; Samuels et al., 2017).

Sesamoids were examined in the postcranial skeleton of specimens from the following collections: American Museum of Natural History (AMNH), Instituto de Bio y Geociencias del Noroeste Argentino, Salta, Argentina (IBIGEO), Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN-Ma), Royal Ontario Museum (ROM), and Princeton University (now housed at the Yale Peabody Museum; YPM-PU). We examined in detail 10 adult specimens of nine yangochiropteran species representing three extant families: *Artibeus planirostris* IBIGEO-M 0216, *Desmodus rotundus* IBIGEO-M 0215, *Carollia perspicillata* MACN-Ma 14247, and *Sturnira lilium* MACN-Ma 18350 / IBIGEO-M 0218 (Phyllostomidae); *Molossops temminckii* MACN-Ma 14151 and *Tadarida brasiliensis* MACN-Ma 22066 (Molossidae); and *Eptesicus furinalis* MACN-Ma 49244, *Dasypterus ega* MACN-Ma 22063, and *Myotis levis* MACN-Ma 14671 (Vespertilionidae).
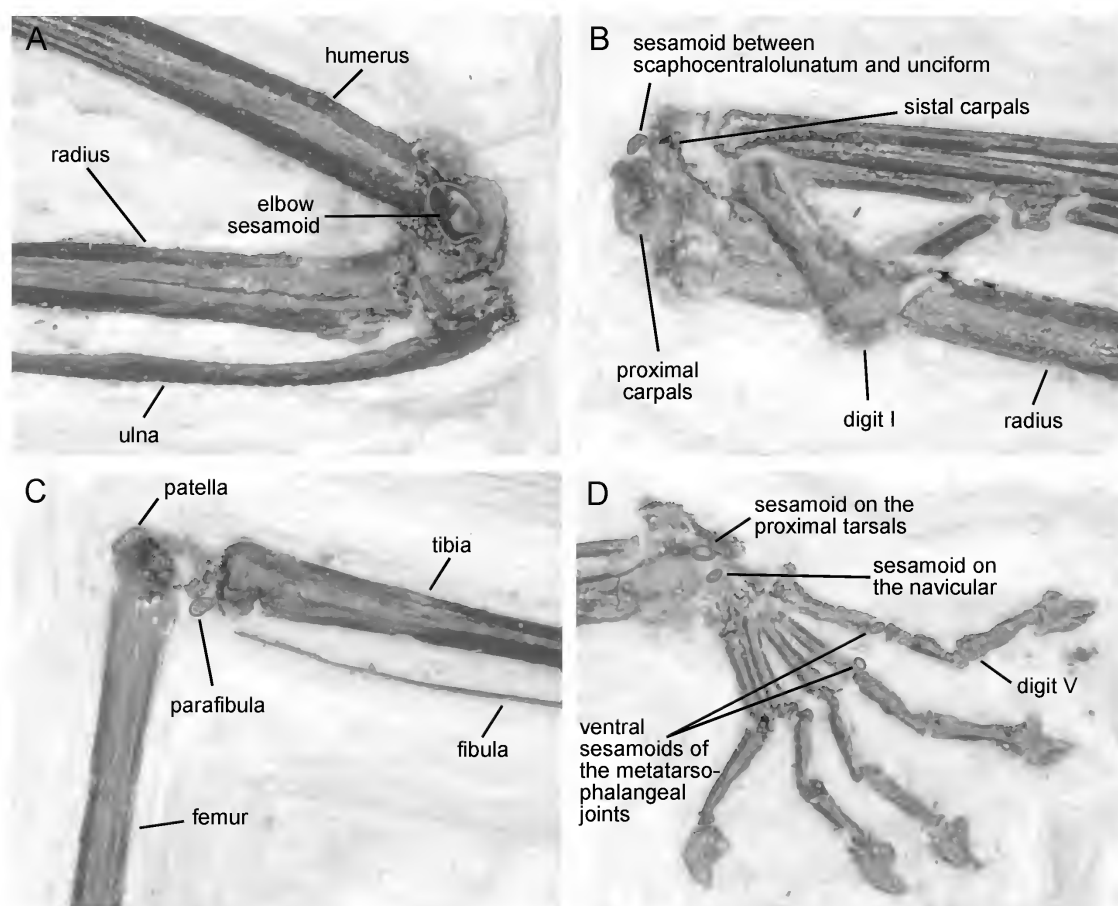
FIG. 1. Eocene bat fossils: *Onychonycteris finneyi* AMNH 142467 showing some of the preserved sesamoids, highlighted with red lines. **A.** Left elbow (dorsal view). **B.** Left carpus (ventral-preaxial). **C.** Left knee (tibial). **D.** Right foot (dorsal).

These specimens were cleared and stained following the protocol of Wassersug (1976), and examined under a Leica stereoscopic microscope with an attached camera with which illustrative photographs were taken. We did not attempt to evaluate intraspecific variation in sesamoid complements due to material limitations and the difficulty of clearing, staining, and dissection. With the exception of *Sturnira lilium* (represented by two individuals found to have identical complements of sesamoids), our samples consisted of one individual only per species. Sesamoid endowment in mammals is known to vary somewhat during ontogeny, with some sesamoids appearing as mineralized structures quite late in adult development (Samuels et al., 2017). This potential source of sesamoid variability was not assessed in our study, although we note that, given the biomechanical demands of flight and the rapid development of adult skeletal morphology in bats, we would not expect much or any variation in sesamoid complements after maturity in bats.

    We also examined sesamoids of two fossil taxa, *Onychonycteris finneyi* ROM55351A, B and AMNH 142467 (Onychonycteridae; Simmons et al., 2008) and *Icaronycteris index* YPM-PU 18150 (Icaronycteridae; Jepsen, 1966), using high-resolution photographs (figs. 1, 2). *Onychonyc-*
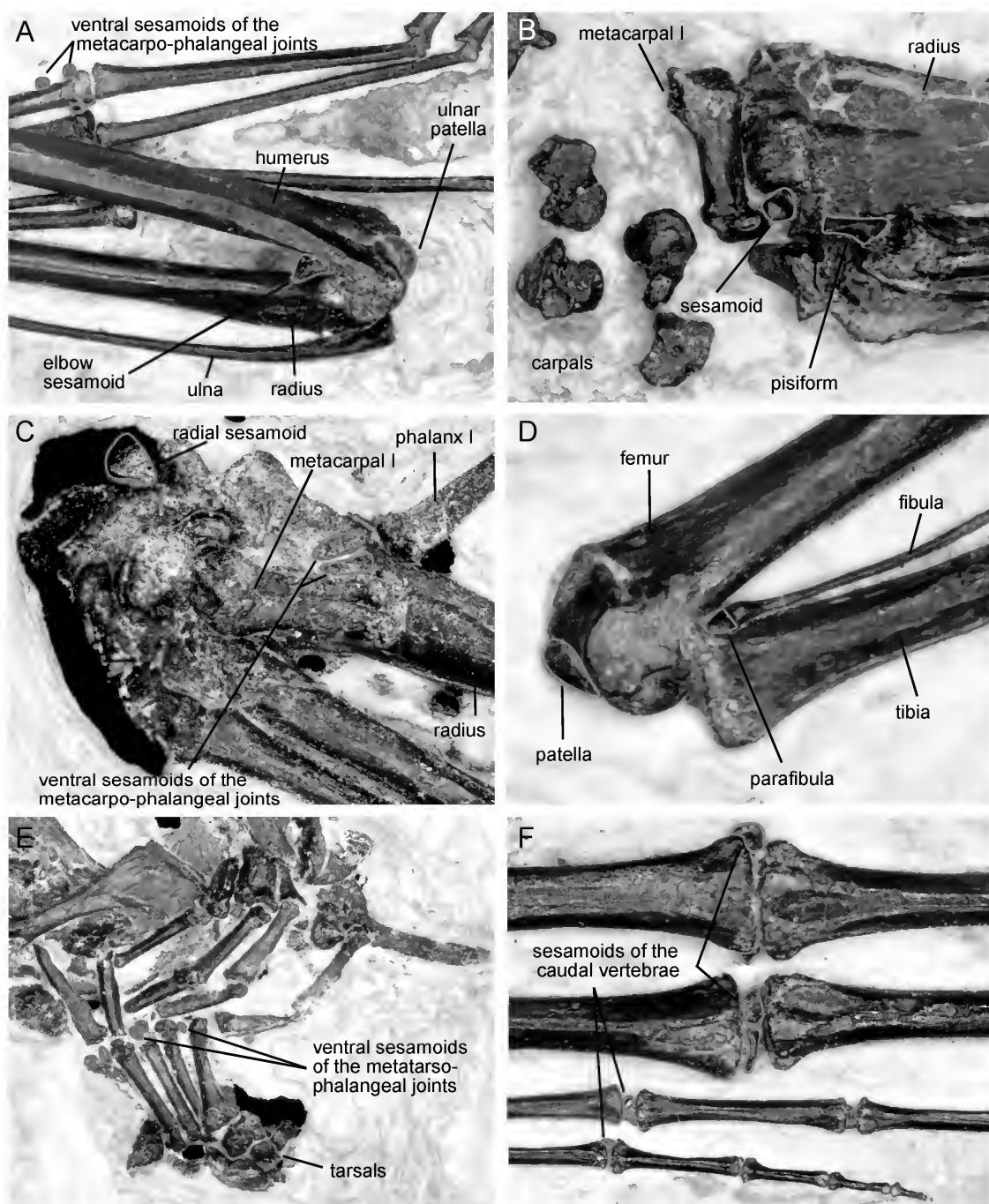
FIG. 2. Eocene bat fossils: *Icaronycteris index* YPM-PU 18150 showing some of the preserved sesamoids, highlighted with red lines. **A.** Left elbow (dorsal view). **B.** Left carpus (dorsal). **C.** Right tarsus (ventral-preaxial). **D.** Left knee (fibular). **E.** Right foot (ventral). **F.** Sequence of caudal vertebrae (dorsal).
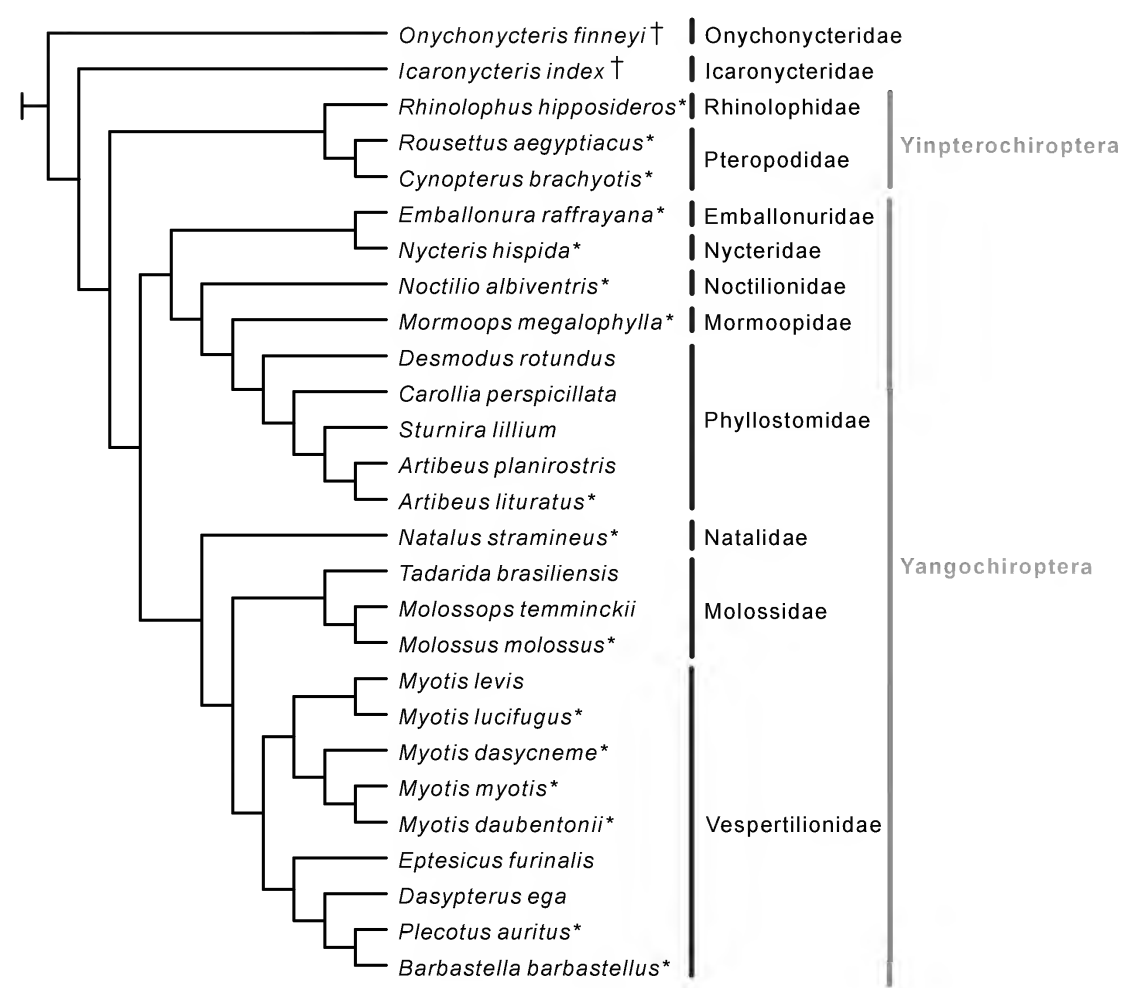
FIG. 3. Phylogeny used in the optimization analysis of sesamoid characters follows relationships proposed by Simmons et al. (2008; extinct taxa indicated with a dagger) and Amador et al. (2018; extant taxa). Species represented in our dataset exclusively by data from autopodial sesamoids compiled from prior studies are indicated with an asterisk (*).

teris finneyi is Late Wasatchian in age (biochronological zone Wa7; late early Eocene, 52.5 mya) from the Fossil Butte Member of the Green River Formation, Wyoming (Simmons et al., 2008). *Icaronycteris index* is of similar age from the same formation (see Smith et al., 2012). These fossil taxa represent the successively most basal lineages of Chiroptera (Simmons et al., 2008).

We coded the presence or absence of each sesamoid or set of sesamoids in each of the 11 taxa that we studied. We also compiled literature data on some autopodial sesamoids (i.e., sesamoids associated with joints in the wrist, hand, ankle, or foot) for 16 additional species (fig. 3; Romanko-wowa, 1961; Norberg, 1972; Cypher, 1996; Reyes-Amaya et al., 2017). These data were combined in a character matrix that included the 46 sesamoid characters listed in table 1. For ancestral states reconstructions, data from the sesamoid matrix was mapped onto a pruned version of the bat phylogeny of Amador et al. (2018; fig. 3) using parsimony as implemented by the program TNT

TABLE 1. Bat sesamoid list. Number (no.), general location (FL, forelimb; HL, hind limb; T, tail), specific location, in parentheses (Pc, pectoral girdle; E, elbow; A, manual/pedal autopodium; Pv, pelvic girdle; K, knee), and character description for each sesamoid or set of sesamoids identified in this paper. Character numbers begin with "0" to accommodate phylogenetic analyses in the program TNT (Goloboff et al., 2008).

No.	Location	Character
0	FL (Pc)	Sesamoid in ligamentum acromioclaviculare, visible in dorsal view
1	FL (E)	Ulnar patella: sesamoid in the insertion of m. triceps brachii just proximal to the reduced olecranon
2	FL (E)	Sesamoid in the origin of m. extensor carpi radialis brevis next to the lateral epicondyle of humerus
3	FL (E)	Sesamoid in the origin of m. supinator and m. extensor digitorum communis next to the lateral epicondyle of humerus
4	FL (E)	Sesamoid in the origin of m. flexor carpi ulnaris on the ventral surface of elbow joint between distal end of humerus and reduced olecranon process of ulna.
5	FL (A)	Sesamoid embedded in the tendon of m. flexor carpi ulnaris next to its insertion
6	FL (A)	Sesamoid in the insertion of m. extensor carpi radialis brevis on the dorsal surface of the wrist between the magnum and the proximal end of metacarpal III
7	FL (A)	Sesamoid near the insertion of m. extensor pollicis brevis on the proximal end of the dorsal surface of metacarpal I
8	FL (A)	Sesamoid on the dorsal surface of wrist between the scaphocentralolunatum and cuneiform
9	FL (A)	Sesamoid on the dorsal surface of wrist between the scaphocentralolunatum and unciform
10	FL (A)	Radial sesamoid: sesamoid on the preaxial side of the ventral surface of wrist, origin of m. abductor digiti quinti in pteropodids and some microbats
11	FL (A)	Pisiform: sesamoid on the ulnar side of the ventral surface of wrist associated with the distal row of carpals
12	FL (A)	Sesamoid on the ventral surface of wrist between the unciform and the proximal end of metacarpal V
13	FL (A)	Sesamoid on the ventral surface of wrist on the trapezium
14	FL (A)	Sesamoid on the ventral surface of wrist between the trapezoid and magnum
15	FL (A)	Sesamoid in the insertion of m. extensor carpi radialis longus in a medial position between the scaphocentralolunatum and trapezium
16	FL (A)	Dorsal sesamoid on the distal end of metacarpal I adjacent to the metacarpo-pahalangeal joint
17	FL (A)	Dorsal sesamoid on the distal end of metacarpal III or III–V adjacent to the metacarpo-pahalangeal joint
18	FL (A)	Dorsal sesamoid on the distal end of the first phalanx of wing digit I just proximal to the ungual phalanx
19	FL (A)	Dorsal sesamoid of the distal end of the second phalanx of wing digits III or III–V
20	FL (A)	Medial ventral sesamoid on metacarpo-phalangeal joint I in the insertion of m. abductor pollicis brevis
21	FL (A)	Lateral ventral sesamoid on metacarpo-phalangeal joint I in the insertion of m. palmaris longus and m. flexor pollicis brevis
22	FL (A)	Pair of ventral sesamoids (lateral and medial) on metacarpo-phalangeal joints III–V
23	HL (Pv)	Sesamoid in the origin of m. rectus femoris on the anterodorsal rim of the acetabulum

TABLE 1 *Continued*

24	HL (K)	Suprapatella(e): a single sesamoid or group of 3 tiny sesamoids on the anterior surface of the distal end of the femur just proximal to the patella
25	HL (K)	Patella: a sesamoid in the insertion tendon of m. quadriceps overlaying the patellar groove of the femur proximal to the cnemial process of tibia
26	HL (K)	Tibial lunula: wedgelike sesamoid on the anterior surface of the knee joint just distal to the patella
27	HL (K)	Two small sesamoids (lateral and medial) on the anterior surface of knee joint
28	HL (K)	One or two lunulae deep inside the knee joint (= ossified meniscus)
29	HL (K)	Parafibula: sesamoid in the insertion of the lateral collateral ligament on the proximal end of the fibula
30	HL (K)	Fabellae: paired sesamoids in the origin of m. gastrocnemius from the femur epicondyles
31	HL (K)	Cyamella: sesamoid in the tendon of m. popliteus near the proximal end of the fibula
32	HL (A)	Dorsal sesamoid associated to the proximal tarsals near the distal tibia-fibula joint
33	HL (A)	Sesamoid in the insertion of the m. tibialis posticus dorsal to the inner cuneiform
34	HL (A)	Sesamoid dorsal to the navicular
35	HL (A)	Sesamoid ventral to the inner cuneiform on the tibial side
36	HL (A)	Small sesamoid between cuboid and the proximal end of metatarsal V on the ventral side
37	HL (A)	One or two small sesamoids (medial and lateral) on the ventral side of the proximal end of metatarsal V
38	HL (A)	Small sesamoid on the ventral side of the proximal end of metatarsal I
39	HL (A)	Plantar sesamoid ventral to the middle point of the metatarsal III
40	HL (A)	Dorsal sesamoid on the metatarso-phalangeal joint of foot digits I–V
41	HL (A)	Dorsal sesamoid on the first-second phalangeal joint of foot digits I–V
42	HL (A)	Dorsal sesamoid on the second-third (ungual) phalangeal joint of foot digits II–V
43	HL (A)	Sesamoidea phalangis: pair of ventral sesamoids (lateral and medial) on metatarso-phalangeal joints I–V in the insertion of mm. interossei and of mm. adductors and abductors of digits I and V
44	T	One or two tiny dorsal sesamoids on or near the joints between a variable number of proximal caudal vertebrae
45	T	One or two tiny ventral sesamoids on or near the joints between a variable number of proximal caudal vertebrae

(Goloboff et al., 2008). We treated the two fossil taxa in our study, *Onychonycteris finneyi* and *Icaronycteris index*, as consecutive outgroups to the chiropteran crown group following Simmons et al. (2008). Sesamoids not observed in the two extinct taxa were coded as "missing" ("?") instead of "absent" because we could not be sure whether they were truly absent in an evolutionary sense or simply missing due to preservation effects. The only sesamoid characters scored as "inapplicable" (coded as "-") were characters 44 and 45 in the case of the phyllostomids *Desmodus rotundus*, *Artibeus planirostris*, and *Sturnira lilium*. These characters describe the sesamoids related to the caudal vertebrae, and the above-mentioned species all have a reduced or absent tail.
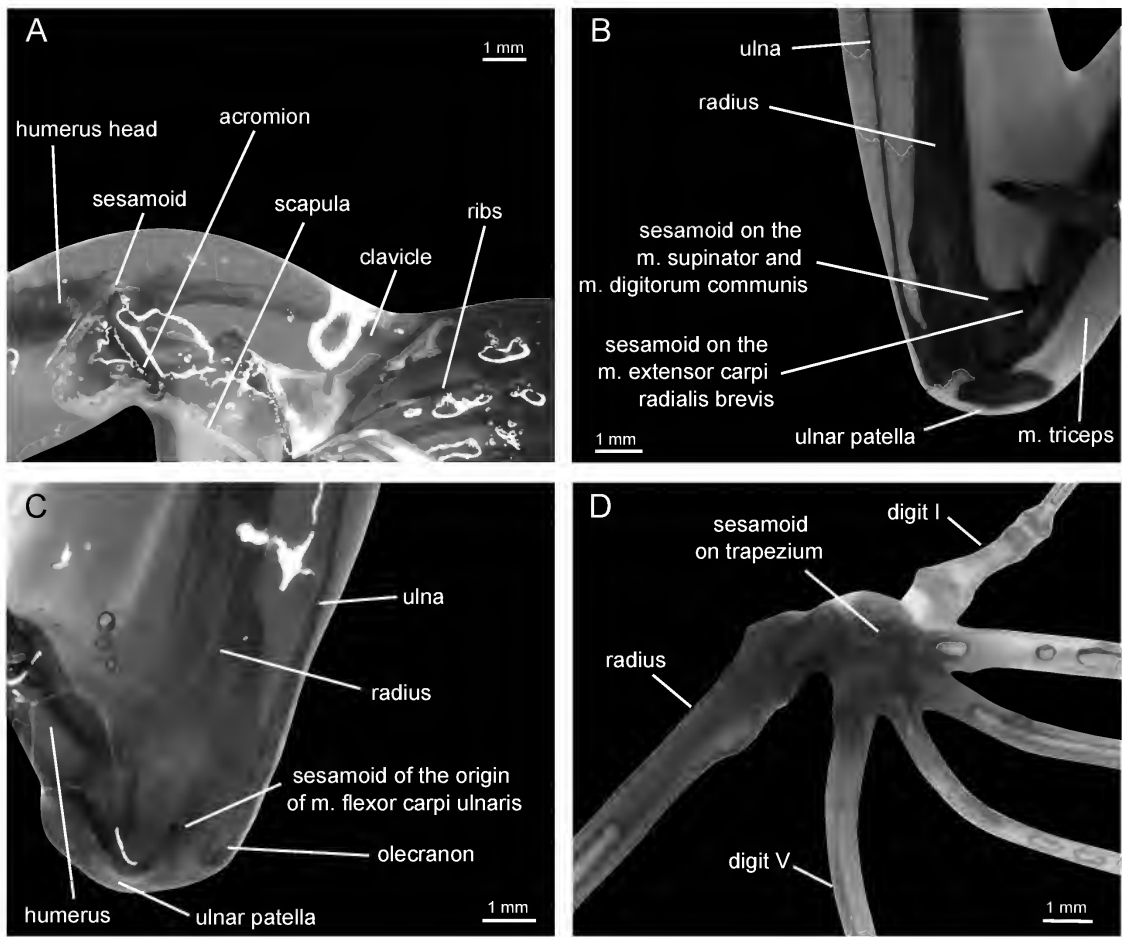
FIG. 4. Selected sesamoids in the forelimb of various extant species. **A.** Left shoulder of *Dasypterus ega* (dorsal view). **B.** Left elbow of *Molossops temminkii* (dorsal). **C.** Left elbow of *Tadarida brasiliensis* (ventral). **D.** Right carpus of *Eptesicus furinalis* (dorsal).

RESULTS

A list of the sesamoids observed in bats, including anatomical position and names (when available), is provided in table 1. In our dissections we observed a total of 46 bat sesamoids or sesamoid series, including 23 in the forelimb (one related to the shoulder joint, four related to the elbow joint, and the remainder related to the autopodial joints; figs. 4, 5), 21 sesamoids in the hind limb (one related to the hip joint, eight to the knee joint, and the remainder to the autopodial joints; figs. 6, 7), and two sesamoid series whose representation is spread across proximal tail vertebrae (fig. 7). Of the 44 sesamoid characters described herein for the limbs, 25 occur in association with extensor muscles and/or extensor surfaces of joints, while the remaining 19 occur in association with flexor muscles and/or surfaces.

A comparison between the sesamoids that we identified and those reported in prior studies is shown in table 2. Most of the sesamoids that we found have been reported at least once in
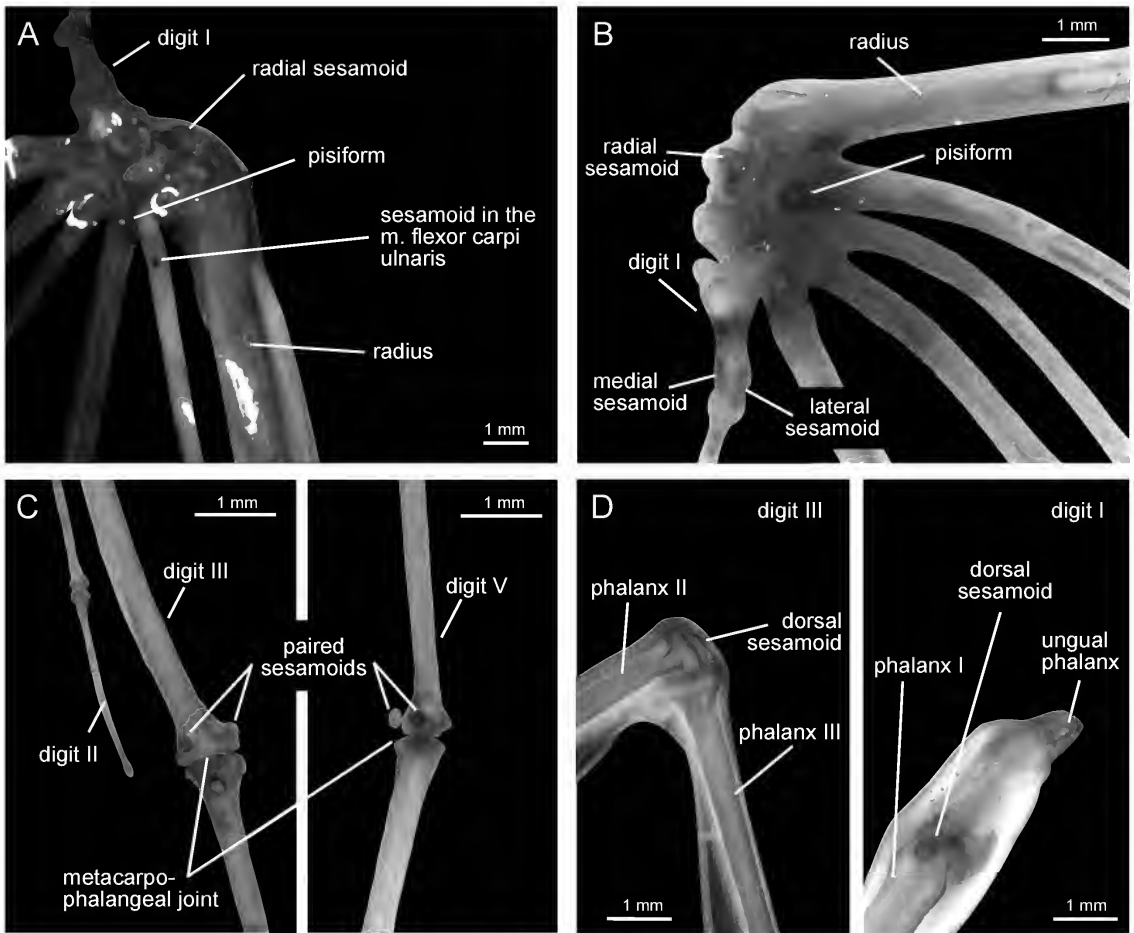
FIG. 5. Selected sesamoids in the forelimb of various extant species. **A.** Right carpus of *Tadarida brasiliensis* (ventral). **B.** Right carpus of *Eptesicus furinalis* (ventral). **C.** Metacarpo-phalangeal joint of wing digits II, III, and V of *E. furinalis* (ventral). **D.** Interphalangeal joints of wing digits III (lateral) and I (dorsolateral) of *Artibeus planirostris*.

previous studies, although often only in passing discussions of other structures (e.g., muscles). However, we found 12 sesamoids not described previously in bats. These include a sesamoid on the dorsal surface of wrist between the scaphocentralolunatum and the unciform (char. 9; fig. 1); a sesamoid on the ventral surface of wrist on the trapezium (char. 13); a dorsal sesamoid on the distal end of second phalanx of wing digits III or III–V (char. 19; fig. 5); the suprapatella (described by Smith et al., 1995, but not referred to as a sesamoid structure; char. 24; fig. 6); the tibial lunula (char. 26; fig. 6); two small sesamoids (lateral and medial) on the anterior surface of knee joint (char. 27); the lunulae (one or two) inside the knee joint (char. 28; fig. 6); the fabellae (char. 30); the cyamella (char. 31); a small ventral sesamoid on the proximal end of metatarsal I (char. 38); and sesamoids associated with the caudal vertebrae (chars. 44 and 45; figs. 1, 7). Table 3 summarizes seven sesamoids mentioned in the literature on bats that were absent in the taxa in our sample. All these sesamoids are autopodial, with four found in
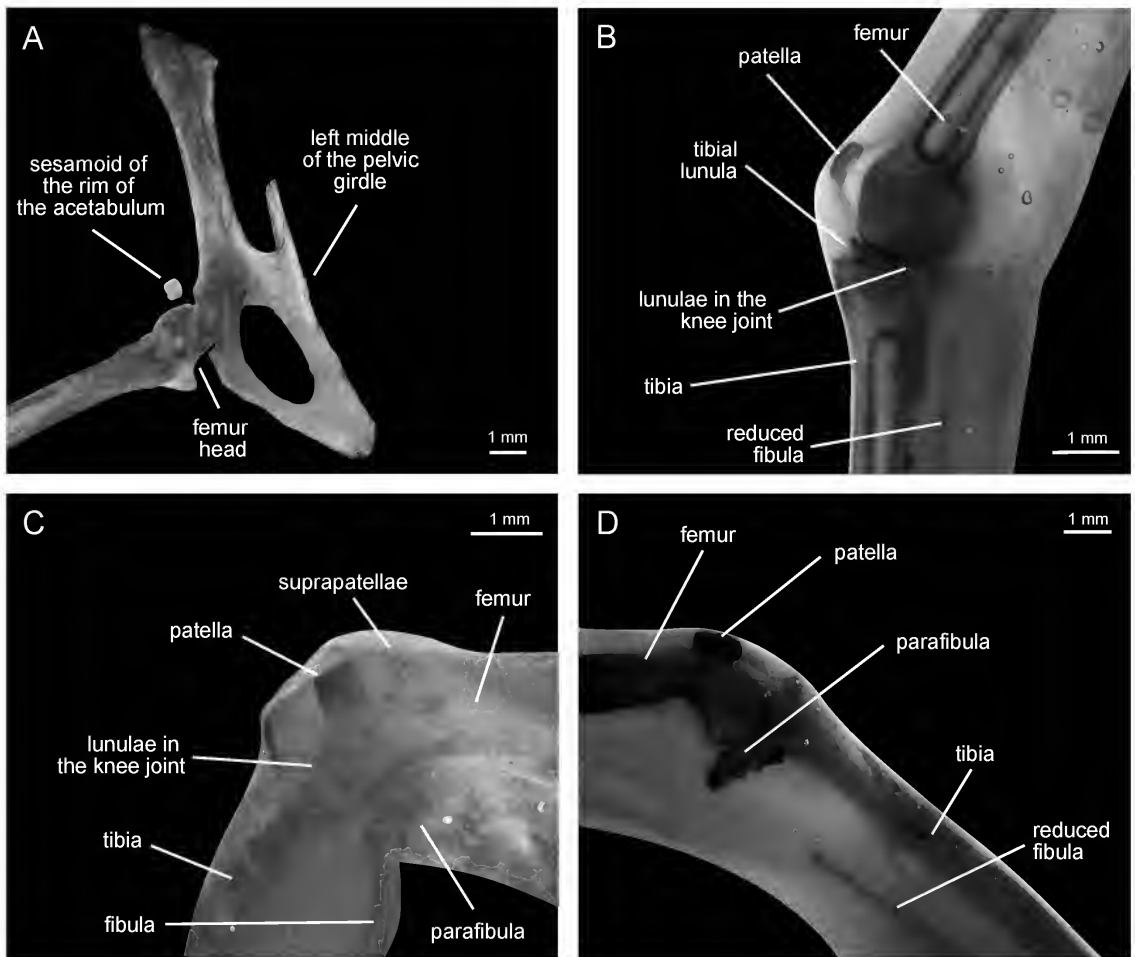
FIG. 6. Selected sesamoids in the hind limb and tail of various extant species. **A.** Left joint between pelvic girdle and femur of *Carollia perspicillata* (dorsal view). **B.** Right knee of *Eptesicus furinalis* (tibial). **C.** Left knee of *Tadarida brasiliensis* (fibular). **D.** Left knee of *Sturnira lilium* (tibial).

the handwing and three in the foot. Among the extant species examined in our study, those exhibiting the greatest number of sesamoids were *Tadarida brasiliensis* and *Molossops temminckii* (23 and 22 sesamoids or sets of sesamoids), both members of the family Molossidae. *Desmodus rotundus* and *Sturnira lillium* (Phyllostomidae) each had 20 sesamoids, and the rest of the species in our study exhibited 15–18 sesamoids or sets of sesamoids (table 4).

Preservation of a large number of minute sesamoid elements in small Eocene bat specimens is truly remarkable. In his description of *Icaronycteris*, Jepsen (1966) reported a total of 44 individual sesamoid elements (many of these representing homologs preserved on both sides of the skeleton); of these he named and figured just two, the pisiform and a "sesamoid of right wrist," which we identified as the radial sesamoid (our char. 10). We positively identified 10 and 12 sesamoids (or sets of sesamoids) in *Onychonycteris* and *Icaronycteris*, respectively (table 4). Five of these, the medial ventral sesamoid on the metacarpo-phalangeal joint I (char. 20), the lateral ventral sesamoid on the metacarpo-phalangeal joint I (char. 21), the
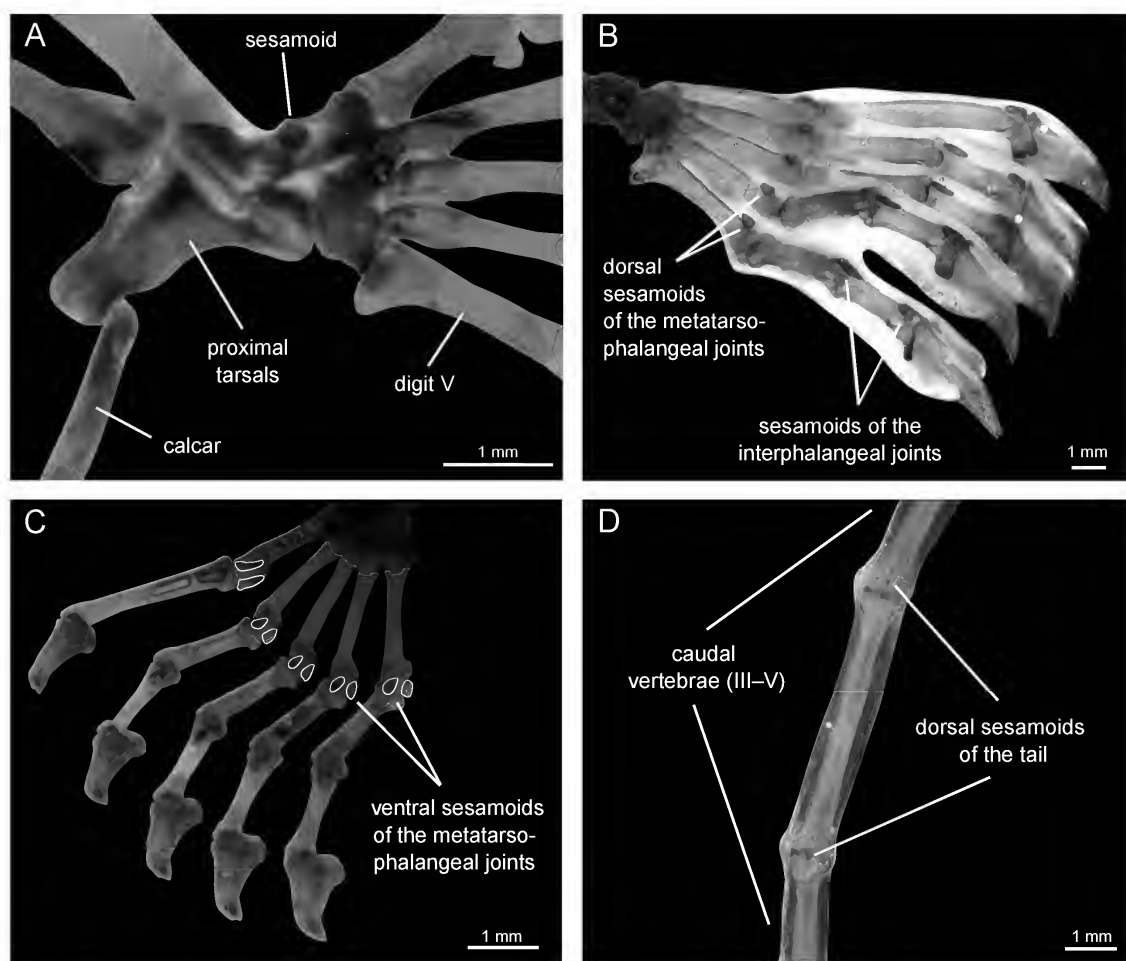
FIG. 7. Selected sesamoids in the hind limb and tail of various extant species. **A.** Right tarsus of *Dasypterus ega* (dorsal). **B.** Right autopodium of *Artibeus planirostris* (dorsal). **C.** Right autopodium of *Eptesicus furinalis* (ventral). **D.** Caudal vertebrae of *E. furinalis* (dorsal).

femoral patella (char. 25), the parafibula (char. 29), and the pedal ossa sesamoidea phalangis (char. 43) were identified in both taxa (table 4). None of the sesamoids were exclusively present in the fossil taxa.

Mapping analyses of the sesamoid dataset (table 4) onto the phylogeny revealed that 34 of the 46 sesamoid characters showed potentially significant evolutionary patterns. Seven sesamoid characters (chars. 13, 18, 19, 24, 26, 39, and 40; fig. 8) were associated with particular chiropteran clades (table 5), hence their presence may represent synapomorphies of the clades in question. However, analyses of a wider taxonomic sample will be necessary to test these observed patterns. Seven sesamoid characters (chars. 10, 11, 20, 21, 22, 25, and 43; fig. 9) were found to be present in all terminal taxa that could be scored, suggesting that they are plesiomorphic for crown Chiroptera. Seven other sesamoid characters (chars. 0, 14, 27, 30, 31, 33, and 38; fig. 10) were found to occur only in one sampled taxon each; these may represent autapomorphies, though, again, greater taxonomic sampling are necessary to test these hypoth-

TABLE 2. Chiropteran sesamoids reported in the present and prior studies. When authors noted the taxa examined, these are listed in parentheses. Character numbers follow table 1.

	This study	Macalister, 1872	Vaughan, 1959	Romankowowa, 1961	Walton and Walton, 1970[a]	Walton and Walton, 1970[b]	Vaughan and Bateman, 1970	Norberg, 1972	Panyutina et al., 2015	Cypher, 1996	Reyes-Amaya et al., 2017
0	–	–	–	–	–	–	–	–	X	–	–
1	X (all species[a])	–	X (Eumops, Myotis)	–	X	X (Pteronotus psilotis)	X (Mormoops megalophylla, Pteronotus parnelli)	X (Rousettus aegyptiacus)	X	–	–
2	–	–	X (Eumops)	–	–	X (Pteronotus psilotis)	X (Mormoops megalophylla)	–	X	–	–
3	–	–	X (Eumops, Macrotus, Myotis)	–	–	–	X (Mormoops megalophylla)	X (Rousettus aegyptiacus)	X	–	–
4	X (Dobsonia)	–	–	–	–	–	–	–	–	–	–
5	–	–	–	X (Myotis myotis)	–	–	–	–	–	–	–
6	–	–	X (Eumops, Macrotus, Myotis)	X (Plecotus auritus, Barbastella barbastella, Myotis dasycneme, M. daubentoni)	X (Phyllostomus hastatus)	–	X (Mormoops megalophylla)	–	X	X (Emballonura raffrayana, Nycteris hispida, Mormoops megalophylla, Molossus molossus, Carollia perspicillata)	–
7	X	–	–	X (all species[b] except Myotis myotis)	X (Phyllostomus hastatus)	–	–	X (Rousettus aegyptiacus)	–	X (Noctilio albiventris, Mormoops megalophylla, Carollia perspicillata, Myotis lucifugus)	–
8	–	–	–	–	X (Myotis myotis)	–	–	–	–	–	–
9	–	–	–	–	–	–	–	–	–	–	–

TABLE 2. *Continued.*

This study	Macalister, 1872	Vaughan, 1959	Romankowowa, 1961	Walton and Walton, 1970[a]	Walton and Walton, 1970[b]	Vaughan and Bateman, 1970	Norberg, 1972	Panyutina et al., 2015	Cypher, 1996	Reyes-Amaya et al., 2017
10[d]	–	X (*Macrotus*)	X (all species[b])	X (*Phyllostomus hastatus*)	–	X (*Mormoops, Pternotus*)	X (*Rousettus aegyptiacus*)	X	X (all species[c])	–
11	–	X (*Eumops, Macrotus, Myotis*)	X (all species[b])	X (*Miniopterus, Rhinopoma, Icaronycteris*)	X (*Pteronotus psilotis*)	X (*Mormoops, Pternotus*)	X (*Rousettus aegyptiacus*)	X	X (all species[c])	–
12	–	–	–	–	X (*Pteronotus psilotis*)	–	–	–	X (*Nycteris hispida, Noctilio albiventris, Mormoops megalophylla, Molossus molossus, Carollia perspicillata, Myotis lucifugus*)	–
13	–	–	–	–	–	–	–	–	–	–
14	–	–	–	X (*Myotis myotis*)	–	–	–	–	–	–
15	–	–	X (*Myotis dasycneme*)	X (*Myotis myotis*)	–	–	–	X (*Nyctalus*)	–	–
16	–	–	X (*Barbastella barbastellus*)	X (*Phyllostomidae*)	–	X (*Mormoops megalophylla*)	–	–	–	–
17	–	–	–	X (*Phyllostomidae*)	–	–	–	–	–	–
18	–	–	–	–	X (*Pteronotus psilotis*)	–	–	–	–	–
19	–	–	–	–	–	–	–	–	–	–
20	–	–	X (all species[b])	X (*Pteronotus psilotis*)	X (*Pteronotus psilotis*)	–	X (*Rousettus aegyptiacus*)	X	–	–
21	X (*Pteropus giganteus*)	–	X (all species[b])	X (*Pteronotus psilotis*)	X (*Pteronotus psilotis*)	–	X (*Rousettus aegyptiacus*)	X	–	–
24	–	–	–	–	–	–	–	–	–	–

TABLE 2. Continued.

This study	Macalister, 1872	Vaughan, 1959	Romankowowa, 1961	Walton and Walton, 1970[a]	Walton and Walton, 1970[b]	Vaughan and Bateman, 1970	Norberg, 1972	Panyutina et al., 2015	Cypher, 1996	Reyes-Amaya et al., 2017
25	–	X (Eumops, Macrotus, Myotis)	–	X	X (Pteronotus psilotis)	–	–	–	–	–
26	–	–	–	–	–	–	–	–	–	–
27	–	–	–	–	–	–	–	–	–	–
28	–	–	–	–	–	–	–	–	–	–
29	X (all species[a] except Nyctalus noctula)	–	–	–	X (Pteronotus psilotis)	–	–	–	–	–
30	–	–	–	–	–	–	–	–	–	–
31	–	–	–	–	–	–	–	–	–	–
32	–	–	X (all species[b] except Myotis dasycneme)	–	–	–	–	–	–	–
33	X	–	–	X	–	–	–	–	–	–
34	–	–	X (Barbastella barbastellus)	–	–	–	–	–	–	–
35	–	X	X (all species[b] except Rhinolophus hipposideros)	–	–	–	–	–	–	X (Desmodus rotundus, Molossus molossus)
36	X	–	–	X	X (Pteronotus psilotis)	–	–	–	–	–
37	–	–	X (Plecotus auritus, Myotis myotis, M. daubentoni)	–	–	–	–	–	–	X (Desmodus rotundus)
38	–	–	–	–	–	–	–	–	–	–
39	–	–	–	–	–	–	–	–	–	X (Molossus molossus)

TABLE 2. *Continued.*

This study	Macalister, 1872	Vaughan, 1959	Romankowowa, 1961	Walton and Walton, 1970[a]	Walton and Walton, 1970[b]	Vaughan and Bateman, 1970	Norberg, 1972	Panyutina et al., 2015	Cypher, 1996	Reyes-Amaya et al., 2017
40	–	–	–	–	X (*Pteronotus psilotis*)	–	–	–	–	X (*Artibeus lituratus*)
41	–	–	–	–	X (*Pteronotus psilotis*)	–	–	–	–	X (*Desmodus rotundus, Artibeus lituratus*)
42	–	–	–	X	X (*Pteronotus psilotis*)	–	–	–	–	X (*Desmodus rotundus, Artibeus lituratus*)
43	–	X (*Eumops, Macrotus, Myotis*)	X (all species[b])	X	X (*Pteronotus psilotis*)	–	–	–	–	X (*Desmodus rotundus, Artibeus lituratus, Molossus molossus*)
44	–	–	–	–	–	–	–	–	–	–
45	–	–	–	–	–	–	–	–	–	–

[a] Species surveyed by Macalister (1872): Pteropodidae (*Pteropus vampyrus, P. giganteus, Macroglossus minimus, Cynopterus sphinx, Dobsonia sp, Rousettus amplexicaudatus*), Rhinolophidae (*Rhinolophus ferrumequinum, R. diadema, R. speoris*), Megadermatidae (*Megaderma lyra*), and Phyllostomidae (*Artibeus jamaicensis, Platyrrhinus vittatus*), Vespertilionidae (*Vespertilio murinus, Pipistrellus pipistrellus, Parastrellus hesperus, Nyctalus noctula, Plecotus auritus, Barbastella barbastellus*).

[b] Species surveyed by Romankowowa (1961): Rhinolophidae (*Rhinolophus hipposideros*), Vespertilionidae (*Plecotus auritus, Barbastella barbastellus, Myotis myotis, M. dasycneme, M. daubentoni*).

[c] Species surveyed by Cypher (1996): Emballonuridae (*Emballonura raffrayana*), Nycteridae (*Nycteris hispida*), Hipposideridae (*Hipposideros diadema*), Noctilionidae (*Noctilio albiventris affinis*), Mormoopidae (*Mormoops megalophylla tumidiceps*), Natalidae (*Natalus stramineus saturatus*), Molossidae (*Molossus molossus crassicaudatus*), Phyllostomidae (*Carollia perspicillata*), Vespertilionidae (*Myotis lucifugus lucifugus*), Pteropodidae (*Cynopterus brachyotis*).

[d] We consider the radial sesamoid (char. 10) to be homologous to the "scaphoid" of Norberg (1972) and Cypher (1996), and to the "prepollex" of Panyutina (2015).

TABLE 3. Sesamoids described in prior studies of bats that were not present in any of the species in our sample. The taxa in which each sesamoid was observed are indicated in parentheses.

	Character	Vaughan, 1959	Walton and Walton, 1970a	Cypher, 1996	Reyes-Amaya et al., 2017
I	Sesamoid of the ventral 4th m. interossei (origin, on the base of metacarpal IV)	X (*Eumops, Macrotus, Myotis*)	–	–	–
II	Sesamoid on the metacarpo-phalangeal joint II (ventral)	–	X (*Pteronotus psilotis*)	–	–
III	Sesamoid dorsal to scaphocentralolunatum-radius articulation	–	–	X (*Hipposideros diadema, Noctilio albiventris*)	–
IV	Sesamoid dorsal to unciform-magnum articulation	–	–	X (*Noctilio albiventris, Mormoops megalophylla, Natalus stramineus, Myotis lucifugus*)	–
V	Tibial ventral sesamoid (on the distal epiphysis)	–	–	–	X (*Artibeus lituratus*)
VI	Calcaneus dorsal sesamoid (on the distal tip)	–	–	–	X (*Molossus molossus*)
VII	Astragalus ventral sesamoid (on the proximal tip)	–	–	–	X (*Artibeus lituratus*)

eses. Eight characters were reconstructed as independent acquisitions (chars. 5, 8, 9, 16, 34, 35, 36, and 41), with four of them (chars. 8, 9, 34, and 36; fig. 11) occurring in one of the two fossil taxa. Finally, five sesamoids were apparently independently lost in different chiropteran lineages (chars. 1–3, 6, and 32; fig. 12).

DISCUSSION

Our survey of sesamoids in Chiroptera indicates that there are roughly similar numbers of sesamoids in the forelimb versus the hind limb, with 23 vs. 21 sesamoids, respectively. In the forelimb, a majority of the sesamoids are located in the autopodium (18, or 78%, in the wrist/hand), while in the hind limb sesamoids are more evenly distributed across joints (only 12, or 57%, in the ankle/foot). In the bat forelimb, muscle bellies are concentrated proximally and they transition more distally into elongated tendons that are associated with multiple supporter and glide sesamoids. The development of this conspicuous tendinous system toward the distal wing may be related to the aerodynamic importance of reducing weight near the tip of the wing (in order to reduce inertial power) since gracile tendons weigh considerably less than heavy muscles (e.g., Norberg, 1990). Fast-running tetrapods, such as felids and horses, also exhibit a trend to develop proximally concentrated muscle bodies that transmit their kinetic forces down through long tendons (Alexander, 1984; Hudson et al., 2011a, 2011b; Cuff et al., 2016). It has been suggested that considerable energy can be stored as elastic strain in these long tendons

Table 4. Sesamoid character matrix by taxon. This data set, including 27 taxa and 46 characters, was used for character optimizations; see Methods for details. In this matrix "0" indicates absence, "1" indicates sesamoid presence, and "?" indicates missing data. Characters are numbered as in table 1.

Species	Character																																													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Onychonycteris finneyi	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	1	1	?	?	?	1	?	?	1	1	1	1	1	?	?	?	?	?	?	1	?	?
Icaronycteris index	?	1	1	?	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	1	1	?	?	?	1	1	?	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?	?	1	1	?
Rhinolophus hipposideros [a]	?	?	?	?	0	0	0	1	2	1	1	0	0	?	?	?	0	?	?	?	1	1	?	?	?	?	?	?	?	?	?	1	1	?	0	0	?	?	0	?	?	0	?	1	2	?
Cynopterus brachyotis [b]	?	?	?	?	0	0	0	0	2	1	1	?	0	?	0	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	1	?	?	0	0	?	?	0	?	?	0	?	1	2	?
Rousettus aegyptiacus [c]	?	?	?	?	2	2	2	2	1	2	1	?	2	?	2	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?
Emballonura raffrayana [b]	?	?	?	?	2	1	2	1	2	2	1	1	0	?	0	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nycteris hispida [b]	?	?	?	?	2	1	0	0	2	1	1	1	0	?	0	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Noctilio albiventris [b]	?	?	?	?	2	0	0	1	2	2	1	1	1	?	0	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mormoops megalophylla [b]	?	?	?	?	2	1	1	1	2	2	1	1	1	?	0	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	2	?	?	?	1	1	?	?	?	?
Artibeus lituratus [d]	?	?	?	?	2	2	2	2	2	2	1	1	?	?	2	?	?	?	?	?	1	1	?	1	?	1	?	?	?	?	?	?	2	0	0	0	0	?	0	?	1	1	1	1	–	–
Artibeus planirostris	0	0	1	0	0	0	1	1	0	0	1	?	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	–	–
Carollia perspicillata	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	
Desmodus rotundus	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	–	–	–
Sturnira lilium	0	1	1	0	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	1	0	1	1	–	–
Natalus stramineus [b]	?	?	?	?	2	0	0	0	2	2	1	1	0	?	2	0	?	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Molossops temminckii	0	1	1	1	1	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0
Molossus molossus [b,d]	?	?	?	?	2	0	1	0	2	2	1	1	1	?	2	0	?	?	2	2	2	1	2	0	2	1	0	2	2	1	2	2	1	0	2	0	?	?	2	1	0	0	0	1	2	?
Tadarida brasiliensis	0	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1
Barbastella barbastellus [a]	?	?	?	?	2	2	0	1	2	2	1	1	0	?	2	0	1	2	0	0	1	1	0	1	0	1	0	1	1	2	2	2	2	0	1	1	2	2	0	0	0	1	2	2	2	2
Dasypterus ega	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Eptesicus furinalis	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	1
Myotis dasycneme [a]	?	?	?	?	2	0	1	1	2	2	1	1	0	?	2	1	0	2	2	2	1	2	1	0	2	2	2	2	2	2	2	2	0	2	0	0	2	2	0	2	0	0	0	1	2	2
Myotis daubentonii [a]	?	?	?	?	2	0	1	1	2	2	1	1	0	?	2	0	0	2	2	2	1	1	2	0	2	2	2	2	2	2	2	1	2	0	0	1	1	2	0	2	0	0	0	1	2	2
Myotis levis	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Myotis lucifugus [b]	?	?	?	?	2	0	0	1	2	2	1	1	1	?	2	0	2	2	2	2	1	1	2	0	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	0	0	0	1	2	2
Myotis myotis [a]	?	?	?	?	2	1	0	0	2	2	1	1	0	?	2	0	0	2	2	2	1	1	2	0	2	2	2	2	2	2	2	1	1	2	0	1	1	2	0	2	0	0	0	1	2	2
Plecotus auritus [a]	?	?	?	?	2	0	1	1	2	2	1	1	0	?	2	0	0	2	2	2	1	1	2	0	2	2	2	2	2	2	2	1	1	2	0	1	1	2	0	2	0	0	0	1	2	2

[a] Romankowowa, 1961.
[b] Cypher, 1996.
[c] Norberg, 1972.
[d] Reyes-Amaya et al., 2017.

TABLE 5. Sesamoid characters apparently present in particular chiropteran clades; see discussion in text. Characters are numbered as in table 1.

Clade	Character
Phyllostomidae	18: Dorsal sesamoid on the distal end of the first phalanx of wing digit I just proximal to the ungual phalanx
	19: Dorsal sesamoid of the distal end of the second phalanx of wing digits III or III–V
Stenodermatinae	40: Dorsal sesamoid on the metatarso-phalangeal joint of foot digits I–V
Molossidae	13: Sesamoid on the ventral surface of wrist on the trapezium
	24: Suprapatella(e)
	39: Plantar sesamoid ventral to the middle point of the metatarsal III
Vespertilionidae	26: Tibial lunula

(Cuff et al., 2016), and the same function may apply to the long tendons in bat wings (e.g., Konow et al., 2015). Regardless, the evolution of the expanded tendinous system in the hand-wing of bats may have been facilitated by the acquisition of sesamoids to aid in the functional organization of the elongated tendons, acting to help avoid bowstringing and/or tendon slippage around joints during the wingbeat cycle. Differences in the relative distribution of sesamoids within the bat forelimb and hind limb may thus be at least partially explained by the specializations of the forelimb for flight.

In the present study, we identified 46 sesamoid characters that correspond to 89 individual elements if all were present in a hypothetical bat (counting one side of the body for limb characters). This is a higher number than any previously identified for any vertebrate; anurans, for example, exhibit variation in 20 sesamoid characters corresponding to 54 individual elements (maximum hypothetical number; Ponssa et al., 2010), while lizards show variation in 41 characters, corresponding to 67 individual elements (maximum hypothetical number; Jerez et al., 2010). This preliminary comparison, based on an admittedly small sample of bats, illustrates the remarkable complement of sesamoids variously found in Chiroptera; future studies including a broader taxonomic sample will likely increase these numbers. Individual bat species also apparently have a large number of sesamoids if we compare the sesamoid endowment of the bat species with the highest number of sesamoid characters scored positively, *Tadarida brasiliensis* with 23 sesamoids (or sets of sesamoids), with the 14 described for dogs (*Canis lupus familiaris*; Evans and De Lahunta, 2013) and the six sesamoids frequently present in humans (*Homo sapiens*; Bizarro, 1921).

Evolution, Function, and Development of Selected Sesamoids

ULNAR PATELLA. The ulnar patella (char. 1) is a large sesamoid associated with the insertion of the tendon of m. triceps. An ulnar patella is present among tetrapods in several groups including anurans (Vickaryous and Olson, 2007; Ponssa et al., 2010), lizards (Jerez et al., 2010), and birds (Barnet and Lewis, 1958; Vickaryous and Olson, 2007). Among mammals, the ulnar patella has been found only in bats (Gunn, 1928; Haines, 1940; Walton and Walton, 1970a) with an
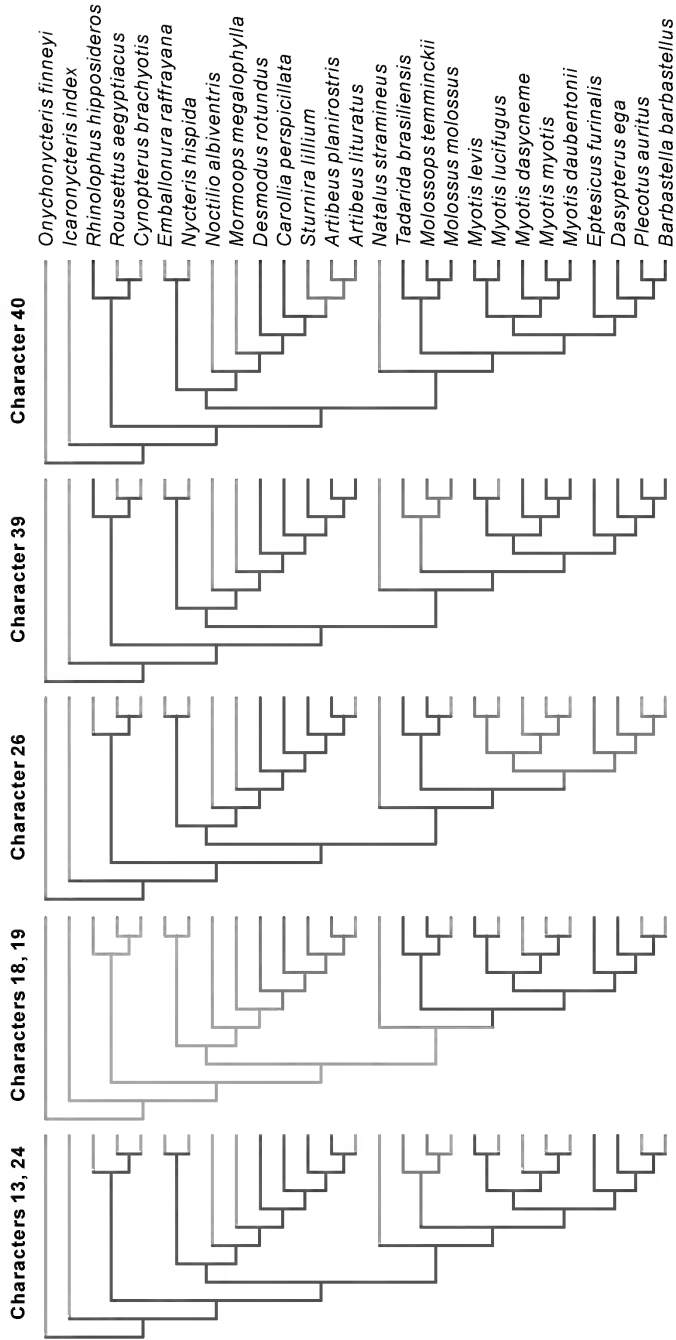
FIG. 8. Optimizations of selected sesamoids that characterize particular clades and which may represent synapomorphies; red indicates presence of the sesamoid in a taxon or clade, blue indicates absence, and gray indicates ambiguity. The topology corresponds to the tree shown in figure 3.
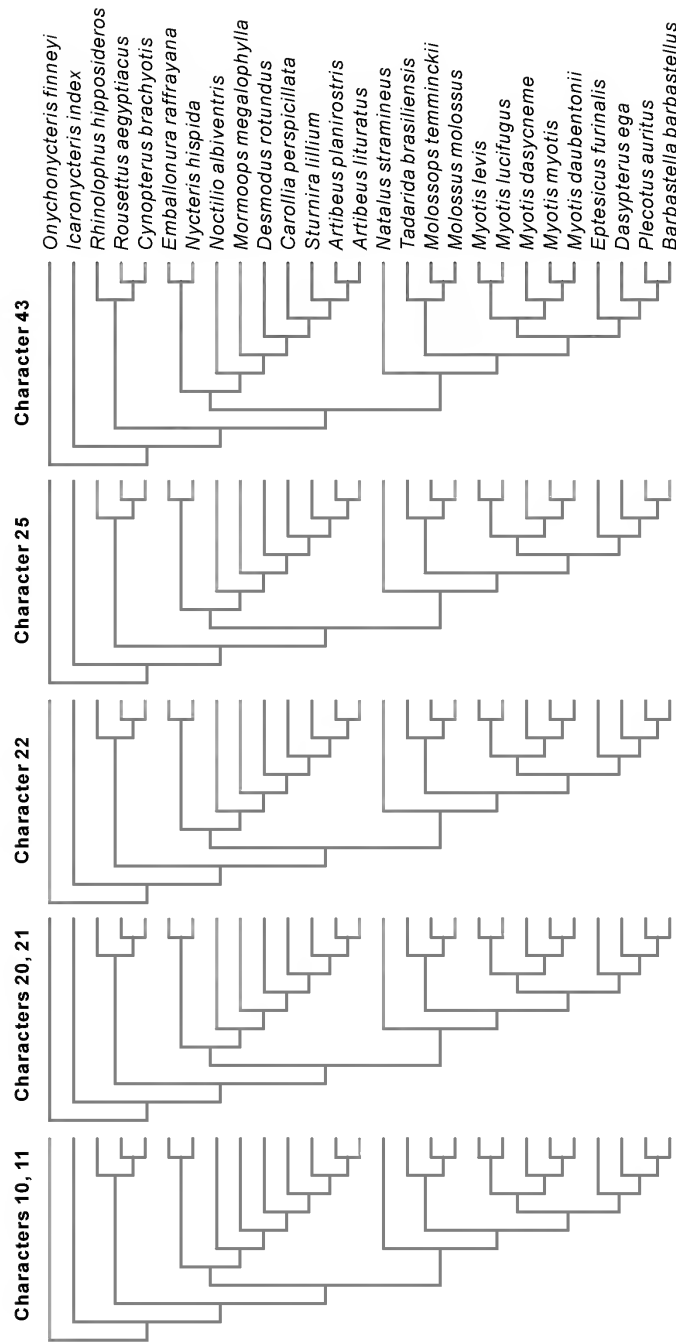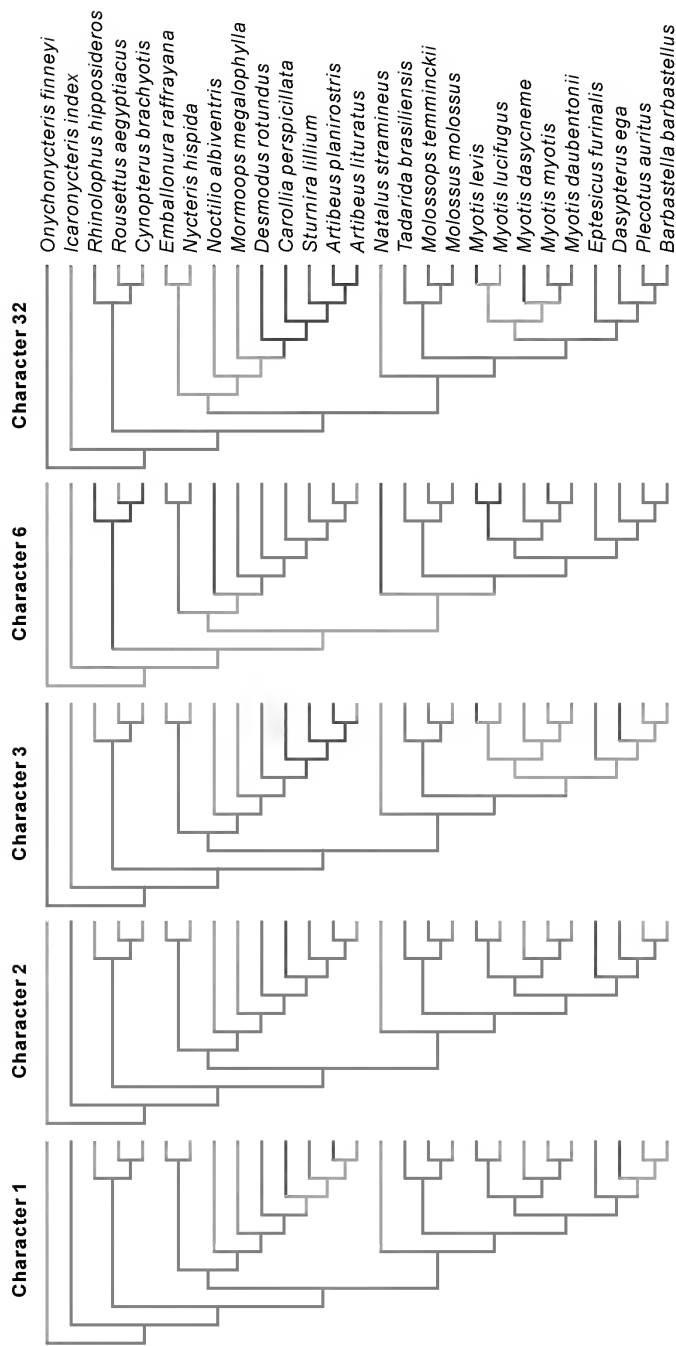
FIG. 9. Optimizations of selected sesamoids interpreted in this study as probable plesiomorphic features of crown Chiroptera; red indicates presence of the sesamoid, and gray indicates ambiguity. The topology corresponds to the tree shown in figure 3.
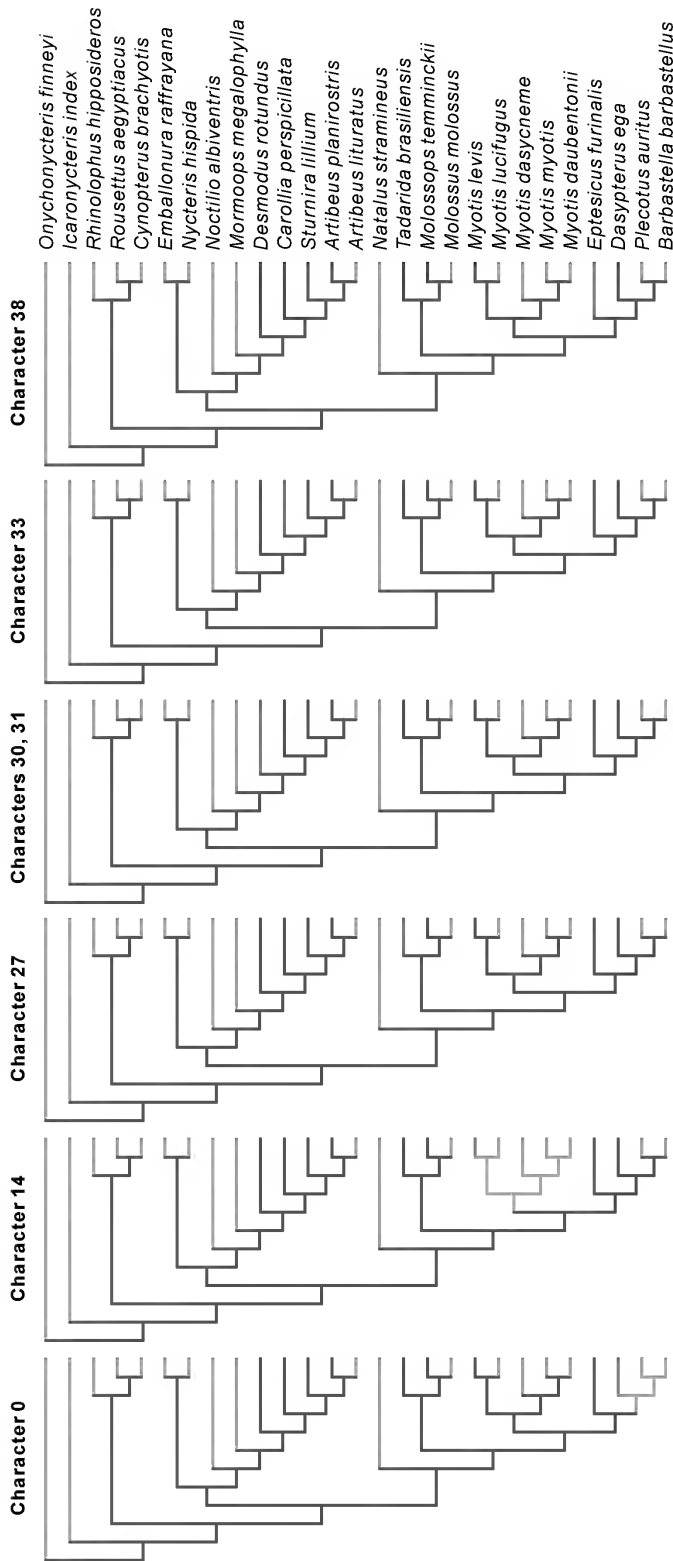
FIG. 10. Optimizations of selected sesamoids found to be present in just one terminal taxon; red indicates presence of the sesamoid in a taxon, blue indicates absence, and gray indicates ambiguity. The topology corresponds to the tree shown in figure 3.
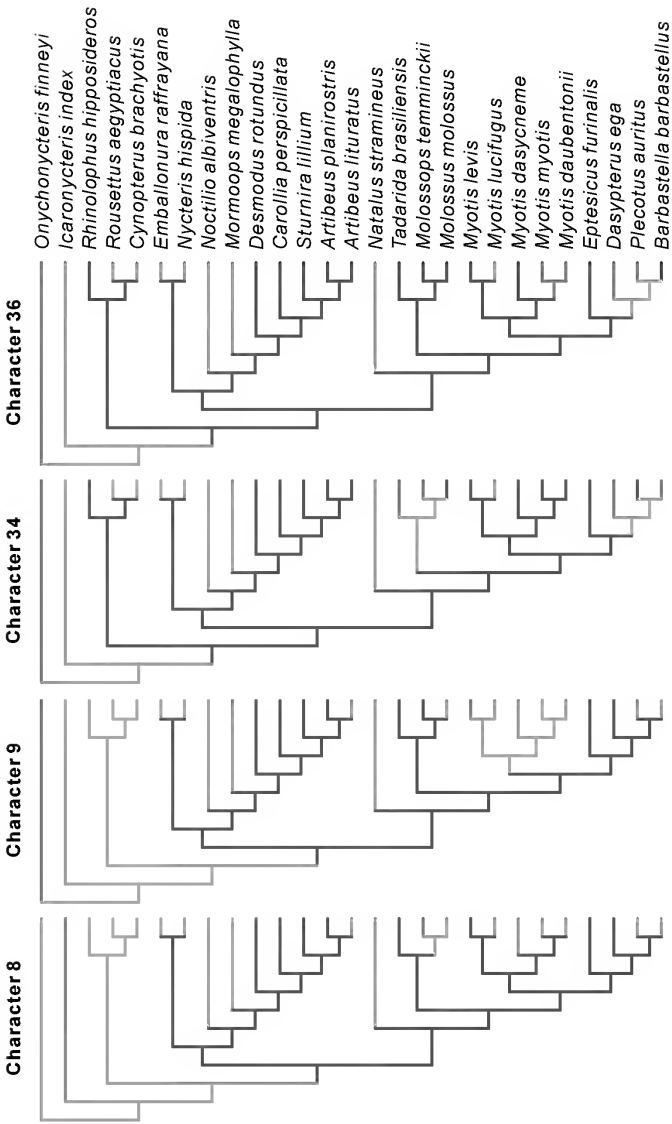
FIG. 11. Optimizations of selected sesamoids that apparently evolved convergently in at least one extant and one extinct bat lineage; red indicates presence of the sesamoid in a taxon or clade, blue indicates absence, and gray indicates ambiguity. The topology corresponds to the tree shown in figure 3.

FIG. 12. Optimizations of selected sesamoids that were apparently lost independently in at least two bat lineages; red indicates presence of the sesamoid in a taxon or clade, blue indicates absence, and gray indicates ambiguity. The topology corresponds to the tree shown in figure 3.

unconfirmed report that it may also be present in some rodents (Hardman, 1949). According to our optimization (fig. 12), the presence of an ulnar patella is plesiomorphic for crown Chiroptera, already present in *Icaronycteris* (fig. 2) and probably also in *Onychonycteris*. In contrast to comments made by Jepsen (1966: 3) in his original description of *Icaronycteris*, where he reported "no trace of sesamoid at end of ulna," we interpreted the bony structure present on the distal end of the humerus as an ulnar patella (fig. 2). The ulnar patella was apparently independently lost in at least three bat lineages including those leading to *Carollia perspicillata*, *Artibeus planirostris* (Phyllostomidae), and *Dasypterus ega* (Vespertilionidae; fig. 12).

Developmental and injury data from humans provide some clues as to the possible evolutionary origins of the ulnar patella. Gunn (1928) and Habbe (1942) were the first to report cases of "patella cubiti" in humans, a condition in which the olecranon is separated from the ulna and the resulting smaller element—the patella cubiti—appears morphologically and positionally similar to the ulnar patella of bats (fig. 13). This anomaly was long treated by the medical profession as the consequence of an injury or an acquired pseudarthrosis (nonmending bone fracture; e.g., Kjelland, 1945; Levine, 1950; see also Mittal et al., 2014). More recently, however, Winter et al. (2006) reported a patella cubiti case but noted that the separated fragment had a smooth surface, suggesting that it is probably the result of a failure in the fusion between the ossification center of olecranon and the rest of ulna during embryogenesis (see also Ahlgren and Rydholm, 1975). A similar developmental pathway, albeit one that has become fixed rather than anomalous, might be responsible for the occurrence of an ulnar patella in bats.

The observations of Winter et al. (2006) seem to agree with the traction epiphysis hypothesis proposed originally by Parsons (1904): the ulnar patella may be homologous to the unfused epiphysis of the ulna. Supporting this hypothesis, Barnet and Lewis (1958) observed that the presence of an ulnar patella was linked to the absence of an olecranon process (i.e., resulting in an abruptly terminated ulna with no proximal projection beyond the joint) in many avian species. Recently, Koyama et al. (2010) have shown that the ulna of mutant mouse embryos lacking all *Hox11* paralogous genes lacks an olecranon process. In its place, an ectopic ulnar patella–like structure associated with the tendon of m. triceps forms in these mice. However, when Koyama et al. (2010) analyzed olecranon development in wild mouse embryos, they found that it did not originate from an independent ossification center that subsequently fused to the ulna; rather, the olecranon formed from a lengthening of the proximal end of the ulna. This developmental process is contrary to what would be expected under the traction epiphysis hypothesis. In any case, interpretations of bony crests and sculpturing resulting from the putative attachment of sesamoids to the main body of long bones (and vice versa) have been frequently posited in the literature (Parsons, 1904; Pearson and Davin, 1921a, 1921b; Bizarro, 1921; Hogg, 1980; Hutchinson, 2002; Hall, 2005; Koyama. 2010; Eyal et al., 2015). Regardless of the developmental process involved, some of the *Hox11* paralogous genes appear responsible for giving rise to either an olecranon process on the ulna when the gene is expressed, or a separated ulnar patella–like structure when the gene is deactivated (Koyama et al., 2010). Changes in *Hox11* genes thus seem to be implicated in the evolutionary acquisitions and losses of the ulnar patella in mammals. The role of *Hox* genes in sesamoid gain and loss was previously
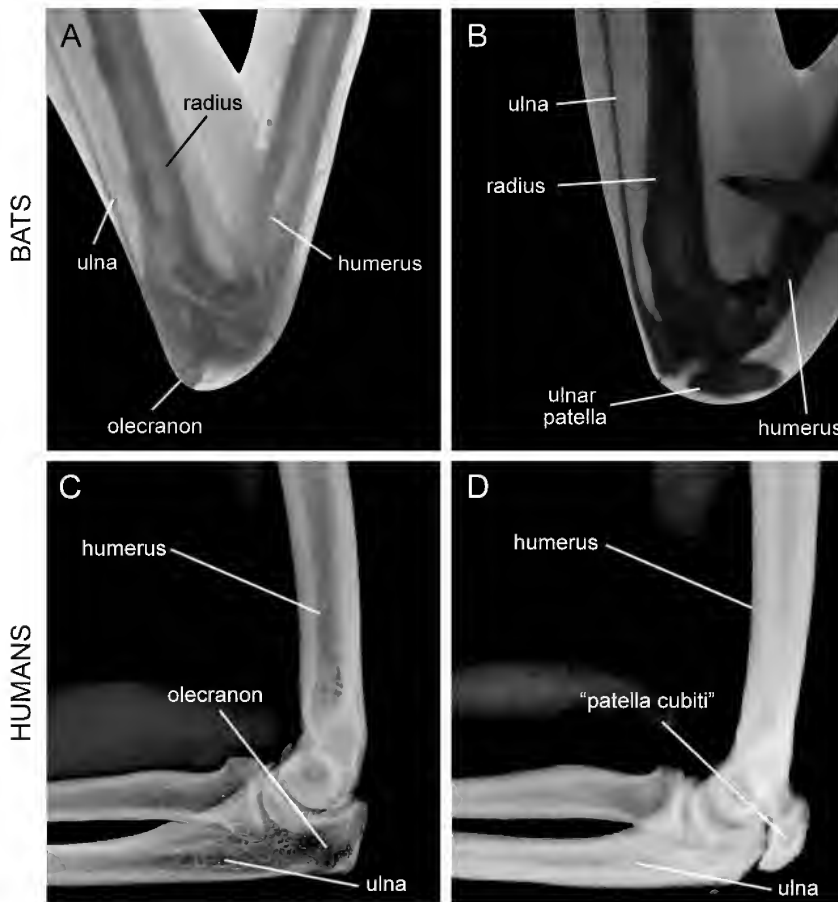
FIG. 13. Comparison between the elbow of bats (**A,** left elbow of *Dasypterus ega*; **B,** left elbow of *Molossops temminkii*) and humans (**C, D**, modified from Mittal et al., 2014), including either an olecranon (**A, C**) or an ulnar patella (**B, D**). The possible homology between the ulnar patella in bats and the anomalous "patella cubiti" in humans is shown.

discussed by Vickaryous and Olson (2007), and more research is clearly needed to determine the role(s) of these genes in general in sesamoid evolution in bats and other tetrapods.

The reduced olecranon process paired with the presence of an ulnar patella in most bat species suggests that m. triceps, whose insertion occurs via the ulnar patella, may be adapted to produce alternative rapid or powerful extension of the forearm depending on the stage in the wingbeat cycle and, therefore, of the joint angle (Vaughan, 1959; Norberg, 1972; Alexander and Dimery, 1985). Electromyographic studies have shown that m. triceps is active primarily as the wing is extended at the top of the upstroke, but the contraction of this muscle continues during the first half of the downstroke (Altenbach, 1979). M. triceps apparently extends the forearm rapidly at the start of the downstroke in order to achieve the maximum thrust and lift from the wingbeat cycle (Vaughan, 1959). This muscle is also important in quick maneuvers that require rapid wing extension (Vaughan, 1959; Maniakas and Youlatos, 2012). Konow et al. (2015) showed that, in *Carollia perspicillata*, elbow flexion at the end of the downstroke actively

stretches the triceps tendon, which then recoils elastically during the upstroke. This springlike mechanism decreases the energy that extensor muscles must expend during upstroke (Konow et al., 2015). The ulnar patella may be acting as a protection for the insertion tendon of m. triceps while it passes over bony prominences at the elbow during rapid wing-extension maneuvers. However, Hermanson and Altenbach (1983) showed that the long and lateral heads of m. triceps in *Antrozous pallidus* are active only during the upstroke, when the elbow joint is flexed, thus contradicting the hypothetical role of m. triceps as elbow extensor. The mechanics of joint and tendon function in bats is clearly complex, and additional biomechanical analyses including a wider taxonomic sampling are necessary in order to clarify the function of m. triceps and the ulnar patella.

PATELLA. The patella (= kneecap; char. 25) in mammals is associated with the tendon of the m. vastus medialis of the quadriceps complex. The function typically assigned to the patella is to protect the m. quadriceps tendon and the underlying patelo-femoral cartilage (Mottershead, 1988), and to hold the tendon further from the joint, thus enhancing the lever system of the knee (e.g., Regnault et al., 2014; Samuels et al., 2017). Although the vastus muscle complex in bats is not differentiated into separate muscle masses (there is only one m. vastus rather than separate m. vastus medialis, m. vastus intermedius, and m. vastus lateralis), a bony patella is present in almost all known taxa (Vaughan, 1959; Simmons and Geisler, 1998) with the exception of *Pteropus* (Smith et al., 1995; see below). The patella was present in all the bats we sampled including fossils (figs. 1, 2, 6, 9), and in our dissections of extant taxa the patella was found to be surrounded by tendinous connective tissue as reported by Vaughan (1959). However, both our extant specimen sample as well as that observed by Vaughan (1959) was restricted to yangochiropteran species.

Smith et al. (1995) analyzed the variation in the patella and associated tissues in 13 bats including 7 members of the family Pteropodidae. In nonpteropodid bats, they observed a bony patella surrounded with tendinous connective tissue just as we found in our study. In three pteropodid species (*Haplonycteris fischeri*, *Cynopterus brachyotis*, *Rousettus aegyptiacus*), Smith et al. (1995) reported a bony patella surrounded by fibrocartilage and hyaline cartilage, but in the remaining four species, all belonging to the genus *Pteropus*, the cartilaginous tissue did not contain any bone structure or evidence of mineralization (Smith et al., 1995). According to the authors, the disposition of this cartilage tissue differs from that in the fibrocartilage patella observed in Macropodidae (i.e., kangaroos and wallabies; Holladay et al., 1990), which occurs in these taxa as a discrete pad that mimics a bony patella in position, size, and shape. In contrast to this arrangement, the cartilage tissue in *Pteropus* is organized as diffuse layers that constitute a relatively undefined structure that is not visible to the naked eye upon dissection. Smith et al. (1995) could not explain this difference in functional terms. These authors suggested that it might be informative to analyze the patella in species with different locomotor habits such *Desmodus rotundus*, which uses quadrupedal locomotion in addition to flight; however, we did not observe any peculiarity in the patella of this species. Instead, we did find an interesting difference in molossids (*Tadarida brasiliensis* and *Molossops temminckii*), which have a suprapatella proximal to the patella, manifested as either a single structure or divided into three adjacent elements (char. 24; fig. 6).

Although many aspects of knee morphology are conserved across Tetrapoda, the structure of the patella shows a notable variation. Anurans, some lizards and birds, and most marsupial mammals have a patella that is composed of fibrocartilage rather than bone (Holladay et al., 1990; Reese et al., 2001; Regnault et al., 2014; Samuels et al., 2017; Abdala et al., 2017; Inamassu et al., 2017). Within crown Mammalia, a bony patella likely evolved between four to six times, and within Eutheria, the bony patella had been lost in three independent lineages: Cetacea (represented by *Tursiops truncatus*), Sirenia (represented by *Trichechus manatus*), and Chiroptera (represented by *Pteropus*) (Samuels et al., 2017). In the former two taxa, the distal hind limb and therefore the patella have been lost during the evolution of adaptations for an aquatic lifestyle. The cause of loss of ossification of the patella in *Pteropus* remains unknown.

Eyal et al. (2015) demonstrated that the patella in mouse embryos originates from a distinct lineage of progenitor cells in the anterodistal surface of the femur, and that posteriorly the patella separates from the femur by the formation of the joint, which is regulated by mechanical load (i.e., this process depends on muscle contractions). These observations appear to refute the epiphysis traction hypothesis of Parsons (1904), in which sesamoids are thought to arise within the tendinous tissue. In contrast, the findings of Eyal et al. (2015) seem to support a contrary hypothesis proposed by Pearson and Davin (1921a, 1921b) who suggested that sesamoids arise from bony processes that become separated from the main bone by a mechanism then unknown. As noted above, a similar mechanism could be acting in the elbow to produce the ulnar patella; therefore, bats constitute interesting study organisms for future work on the ontogeny of major sesamoid elements.

RADIAL SESAMOID AND PISIFORM. The radial sesamoid (char. 10) is located on the radial side of the ventral surface of the wrist, and this element is the origin of m. abductor digiti quintii in many bat species (table 1; fig. 5). This muscle helps stabilize metacarpal V against air pressure created during the downstroke, and is also a weak flexor of digit V, thus helping to regulate camber in the distal part of the wing (Vaughan, 1959; Norberg, 1972). In contrast, the pisiform (char. 11; fig. 5) is also located on the ventral surface of the wrist, but on the ulnar side associated with the distal row of carpals. The distal end of the pisiform is strongly bound by fascia to the proximal end of the metacarpal V, while the proximal end of the pisiform rests against the ventral surface of the trapezium and is bound to the ventral surface of the carpus by connective tissue, allowing little dorsoventral movement (Vaughan, 1959). The pisiform is attached to the radial sesamoid by a broad ligament, the flexor retinaculum. The radial sesamoid is, in turn, the insertion point of the m. abductor pollicis longus. In most mammals, this muscle is inserted into metacarpal I and functions as an abductor of the thumb, but in bats the action is exerted on metacarpal V, via the radial sesamoid and the pisiform (Vaughan, 1959; Noberg, 1972). The action of m. abductor pollicis longus, similar to that of m. abductor digiti quinti, consists in reinforcing the fifth carpometacarpal joint during the downstroke, thus avoiding the dorsal extension of digit V. Additionally, the pisiform serves as an insertion point for the m. flexor carpi ulnaris, which acts as a posterior flexor of digit V (Vaughan, 1959; Norberg, 1972). Even though the radial sesamoid/flexor retinaculum/pisiform complex performs some distinct functions in bats, it also plays a role shared with other tetrapods to form the

carpal tunnel through which the flexor tendons of the forelimb cross the carpal joint and become organized, thereby avoiding the bowstringing of tendons and/or adding to their slippage (Haines, 1950; Fontanarrosa and Abdala, 2014, 2016). This role may be of particular importance in bats because of the conspicuous system of ropelike tendons that must cross the wrist in the handwing. Both a radial sesamoid and a pisiform are present in all the extant bat species we examined, in *Icaronycteris*, and possibly also in *Onychonycteris* (fig. 9), and hence the presence of both elements appears to be plesiomorphic for bats.

PARAFIBULA. The parafibula (char. 29; figs. 1, 2, 6) is located on the proximal end of the fibula within the lateral collateral ligament that connects the femur and the tibia. A fibula with a hypertrophied epiphysis apparently resulting from a fused parafibula has been identified in several extant and extinct mammals (e.g., Barnet and Lewis, 1958; Li and Luo, 2006, Yuang et al., 2013). The parafibula is present as a separate sesamoid in the extinct and most extant bat species observed, with the exception of *Myotis levis* and *Eptesicus furinalis*. We found a parafibula in species with a complete fibula (e.g., *Tadarida brasiliensis*) as well as in species with a reduced fibula (e.g., *Sturnira lilium*) bearing a thin epiphysis (fig. 6). The absence of a parafibula in some species with a reduced fibula (i.e., in *Myotis* and *Eptesicus*) suggests that the parafibula can be lost without any trace of fusion with another bone element, with its reduction occurring either prior to or coincident with fibular reduction. This suggests that the traction epiphysis hypothesis of sesamoid loss (Parsons, 1904) may not be applicable to all cases of sesamoid loss, and that other mechanisms should be considered in future research and discussions.

SESAMOIDS AND QUADRUPEDAL LOCOMOTION

We hypothesize that the relatively high number of sesamoids recorded in molossids (22–23 sesamoids) and vampires (20) may be associated with quadrupedal locomotion in these taxa. The common vampire bat *Desmodus rotundus*, a highly specialized sanguivorous species, combines a symmetrical walk with a particular asymmetrical bounding gait at higher speeds, allowing it to follow prey that move during a feeding event (Riskin et al., 2006). *Desmodus* was the only sampled taxon found to have a cyamella (sesamoid in the m. popliteus) and fabellae (pair of sesamoids in the m. gastrocnemius). Molossids are agile flyers but are also nimble crawlers that use quadrupedal locomotion in their roosts, having a particular wing-folding mechanism that allows them to compactly fold the long wings in order to avoid membrane damage during quadrupedal locomotion (Vaughan, 1966; Schutt and Simmons, 2006). The sesamoids present exclusively in Molossidae (suprapatella and ventral sesamoids on carpus and metatarsus) might be related to this type of locomotion. Chadwick et al. (2017) showed that the patellar tendon of the ostrich, which typically has two patellae (Macalister, 1864), has the potential for developing multiple patellae based solely upon mechanical stimuli. In a similar way, the possible distinctive loading and stress patterns of the patellar tendon in molossids might be favoring the presence of one or more suprapatellae in these taxa. Differences in the properties of tendons playing different functional roles—e.g., those that power locomotion versus those that act to limiting excessive flexion of joints—have been reported in other vertebrates (e.g., Zhang et al., 2017), and the same may apply to sesamoids. Thus, the rela-

tively large number of sesamoids in molossids and *Desmodus* might result from the additional functional demands resulting from regularly employing two very different types of locomotion (i.e., flapping flight vs. quadrupedal cursorial locomotion), a hypothesis first proposed by Reyes-Amaya et al. (2017). In this context, it would be useful for future studies to assess the sesamoid endowment of other quadrupedal bat species such *Mystacina tuberculata* (Mystacinidae) and the two other species of vampires (*Diaemus youngi* and *Diphylla ecaudata*) as well as additional molossid species. *Sturnira lilium* (Phyllostomidae) also shows a high number of sesamoids (20). Based on its sesamoid endowment, as well as the lack of a tail membrane and the notable hind limb dexterity that this species displays when captured, we hypothesize that *S. lilium* might be specialized for quadrupedal locomotion along internal branches of small trees and shrubs while searching for fruit not displayed on the outer branches. Additional investigations of phyllostomids with different locomotor habits might provide further insight into the evolution of sesamoids in this diverse group.

Sesamoids in Fossil Bats

We positively identified 10 and 12 sesamoids (or sets of sesamoids) in *Onychonycteris* and *Icaronycteris*, respectively (table 4, figs. 1, 2). Five of these, the medial ventral sesamoid on the metacarpo-phalangeal joint I (char. 20), the lateral ventral sesamoid on the metacarpo-phalangeal joint I (char. 21), the femoral patella (char. 25), the parafibula (char. 29), and the pedal ossa sesamoidea phalangis (char. 43) were identified in both taxa (table 4). No sesamoid was exclusively present in the fossil taxa. Interestingly, the two fossil bats examined in our study bear a resemblance to molossid bats in terms of their complements of sesamoids. *Onychonycteris* shares eight sesamoids with *Tadarida* and *Molossops*, two of which were almost exclusively found in these species: the elbow sesamoid in the origin of the m. supinator and m. extensor digitorum communis (char. 3), and the sesamoid dorsal to the navicular (char. 34). We hypothesize that this apparent case of convergence may reflect a certain degree of quadrupedal locomotion in *Onychonycteris* (e.g., along tree branches). Both the presence of claws on all wing digits and the limb proportions of *Onychonycteris* suggest that this extinct bat was more similar to other climbing mammals than any other known bat (Simmons et al., 2008). The other Eocene bat that we sampled, *Icaronycteris*, shares 11 sesamoids with *Tadarida* and *Molossops*, of which one sesamoid is exclusively shared in our sample with the latter taxon, namely, the dorsal sesamoid of the wrist, located between the scaphocentralolunatum and the cuneiform (char. 8). It is possible that the presence of these sesamoids in these ancient bats is indicative of similar diverse locomotor habits, but further evaluation of such hypotheses is beyond the scope of the present study.

CONCLUSIONS

Bats possess a very large complement of sesamoids (as many as 23 in a single species) with a large amount of variation among taxa—46 different sesamoids (or sets of sesamoids) occur in Chiroptera. Sesamoid presence is relatively balanced between forelimb and hind

limb; however, when the joints of both limbs are compared, sesamoids are more numerous in the knee than in the elbow, and more so in the manual than in the pedal autopodium. The elbow and knee joints are characterized by embedded sesamoids, while in the autopodial joints we found that supporter and glide sesamoids are more frequent. In the forelimb, a majority of the sesamoids are found in the handwing, possibly associated with the evolution of a conspicuous tendinous system that distally replaced heavy muscle bellies in bats; this system evolved perhaps in response to the aerodynamic need for decreased weight near the wing tip, which in turn facilitates a low inertial power, one of the components of total aerodynamic power required for flight.

All of the sesamoids widely distributed among bat taxa were already present in at least one of the two Eocene species included in our study, indicating that their presence and possibly their function(s) have remained stable at least since the Early Eocene. Most of these ubiquitous sesamoids are plesiomorphic for Chiroptera within the framework of what is known about mammalian sesamoid distributions, with the notable exception of the ulnar patella. This structure, which is apparently absent in other mammals, is known from other tetrapods and hence represents either an evolutionary reversal (if present in the ancestor of tetrapods) or independent acquisitions in particular tetrapod lineages. Other sesamoids are seemingly exclusive to chiropteran clades, although this may be challenged in the future with additional sampling within a wider taxonomic framework. The sesamoid similarities between the two ancient bats and extant molossids may reflect similar functional constraints; however, more work on the functional roles of sesamoids in general, and sesamoids shared among species in particular, will be necessary before we can speculate further on the evolutionary origins and roles of these structures. Most notably, detailed biomechanical studies are needed to test hypotheses of the link between form and function of sesamoids in the chiropteran postcranium. The significant abundance and variability of sesamoids in Chiroptera suggest that bats may provide an excellent model system for enhancing understanding of the function, developmental basis and mechanical significance of sesamoids. This study constitutes an initial step in that direction.

ACKNOWLEDGMENTS

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